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UPWELLING AND FISH PRODUCTION

by

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UPWELLING AND FISH PRODUCTION

by

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FOOD AND AGRICULTURE ORGANIZATION OF THE UNITED NATIONS
Rome, June 1969

PREPARATION OF THIS DOCUMENT

This document has been prepared by D.H. Cushing of Lowestoft following proposals made at the 1967 and 1968 sessions of FAO's Advisory Committee on Marine Resources Research.

A major part of the work of the Fishery Resources and Exploitation Division of FAO's Department of Fisheries is concerned with the appraisal of the world's fishery resources. This appraisal has been carried out as the Division's contribution to FAO's Indicative World Plan. A meeting of consultants concerned with this work underlined the close connection between upwelling areas, areas of high primary production, and rich fishing grounds. The 4th Session of the Advisory Committee on Marine Resources Research (Res. 3.2.2) decided that it would be useful to request selected experts to prepare comprehensive essays on the present knowledge of physical, biological and fishery aspects of upwelling.

ACMRR also noted that a seminar sponsored by UNESCO/IOC and FAO might permit analysis of the questions raised by the IWP Working Party. Some members felt that at this stage it would be more useful to request selected experts to prepare comprehensive essays on present knowledge of physical, biological and fishery aspects of enrichment, for ultimate publication in a single volume by UNESCO and FAO.

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UPWELLING AND FISH PRODUCTION

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1. INTRODUCTION

It has long been known that the upwelling areas in the oceans are rich and that large fish populations live there. The annual catch of anchoveta off Peru of about 8 million (M) tons grew very sharply and there are still enough fish to support the birds. Much of the world's coastline in subtropical seas is in upwelling areas; here fish live in profusion, belying the myth of tropical deserts in the sea. This paper is an attempt to estimate the potential yield from the upwelling areas of the world.

2. THE PHYSICAL BACKGROUND

In each ocean there are two subtropical anticyclones, one north and one south of the equator. In each, the western boundary current is swift, narrow and intense (up to 4 knots in the northern hemisphere) and the eastern boundary current is broad and slow (about ½ knot) and it tends to be somewhat reduced in salinity because it originates in rainy areas. There is upwelling on the eastern boundaries where the winds tend to blow parallel to the coast towards the equator (Wooster and Reid, 1963). Our first generalization is that upwelling is found in the eastern boundary currents of the subtropical anticyclones (Hutchinson, 1950). Except in the special case of the Somali Current, the western currents are too stable to allow upwelling to take place on the scale found in the eastern currents. In higher latitudes where the circulation is cyclonic and when the wind blows parallel to the coast, it intensifies the cyclonic circulation and makes upwelling unlikely. The second generalization, justified in section 3, is that the biological effectiveness of upwelling is confined to the tropics and subtropics. Upwelling areas tend to lie off desert country and the coastal climate is at times foggy and at times windy.

As the water is blown offshore at an angle to the coast it is moved towards the equator. At about 100 km offshore there is often a convergence where the water sinks and, a little further offshore, a divergence, generating a secondary source of upwelling above the thermocline (Hart and Currie, 1960). There are often large swirls in fixed positions, between local upwelling systems (Reid, Hoden and Wyllie, 1958). The current flowing towards the equator is compensated by a countercurrent below about 200 m flowing towards the pole (Gunther, 1936; Reid, Hoden and Wyllie, 1958; Hart and Currie, 1960). Further, there may be narrow surface countercurrents generated inshore during the period of upwelling (Reid, Hoden and Wyllie, 1958; Wyrtki, 1963). The depth of the whole upwelling system is shallow and its offshore boundary is imprecise.

Figure 1 is a diagram of an ideal vertical section through an upwelling area (adapted from Hart and Currie, 1960 and Bang, in press). Above 200 m the water moves towards the equator and the upwelling system lies within this zone; below it the countercurrent moves towards the pole. The coastal upwelling is bounded between 50–100 km offshore by a cell of convergence and divergence. This is the region which Sverdrup (1938) put his dynamic boundary. Inshore of this boundary there is a region of slow mixing of old and new upwelled waters, and offshore of it there is a region of divergence, a secondary form of upwelling. The "roller bearing" of convergence and divergence (Hart and Currie, 1960) is also an agent of offshore transport. The secondary upwelling offshore of this boundary is associated with the wind stress alone, and is generated by the vorticity of the wind stress. The divergences along the equator and elsewhere are created by the same agency (Hidaka, 1958). More recently Yoshida (1967) has attempted to unify the two phenomena, secondary upwelling and coastal upwelling, in one theoretical frame. There tend to be divergences along the poleward boundary of the subtropical anticyclones, at the western ends of the equatorial currents and along the equatorial boundary of the southern anticyclones; similarly there are convergences along the eastern equatorial currents, particularly in summer along the equatorial boundary of the northern anticyclone (Hidaka and Ogawa, 1958). But there are also upwelling areas where the equatorial currents are formed; the Costa Rica Dome is the most well known, at the root of the North Equatorial Current in the North Pacific, but there are analogous phenomena in the East Atlantic and East Indian Oceans.

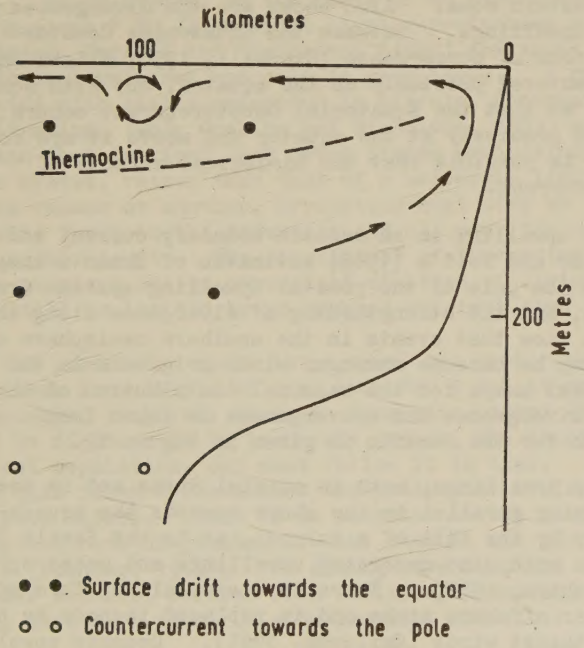

Figure 1. A diagrammatic vertical section of an upwelling area. The full line represents the upwelling and offshore drift to the "roller bearing" of convergence and divergence at about 100 km. Because the upwelling system drifts towards the equator, the upwelled water moves outwards at a slight angle to the coast.

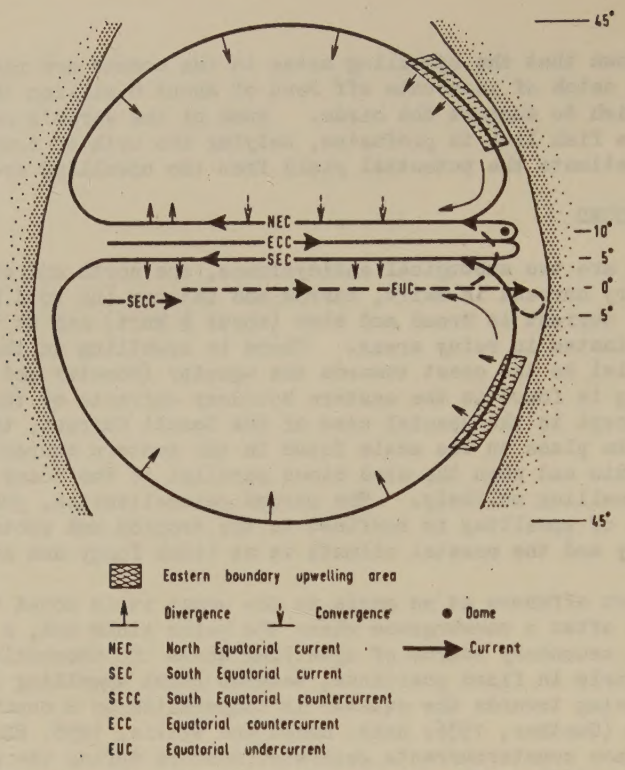

Figure 2. Diagram of the distribution of upwelling in an eastern boundary current.

Figure 2 is a diagram of the upwelling systems in an ideal ocean, based on observations in the Pacific showing the coastal upwellings in the eastern boundary currents, the divergences and convergences in the equatorial current system and the eastern dome. Also shown are the divergences on the poleward boundaries and offshore of the coastal upwellings. Between the Equatorial Countercurrent and the North Equatorial Current there is a zone of convergence (Cromwell, 1958; Hidaka and Ogawa, 1958 and Wyrtki, 1966). The system is not centered precisely on the equator, but with some seasonal variation, is offset somewhat to the north, so that the Equatorial Countercurrent occurs between 5° and 10°N. The Cromwell Undercurrent lies precisely at the equator and above it are found the divergences in the South Equatorial Current; it is possible that the biological effects of divergence are enhanced by upwelling above the Undercurrent.

Figure 3, is a diagram of the seasonal cycle of upwelling in an eastern boundary current and in the equatorial system. It is based partly on Wooster and Reid's (1963) estimates of Ekman transport normal to the coast. It shows the movement towards the pole of the coastal upwelling systems from spring to autumn as the subtropical high intensifies, and the strengthening of divergence along the equator in winter and spring. The diagram does not show that events in the southern hemisphere are bigger and more persistent, which they are. This may be because stronger winds originate in the Southern Ocean, or because the coastlines have the best shape for the seasonal distribution of the direction of the trade winds. The distribution of divergences and convergences is taken from Hidaka and Ogawa's (1958) charts, an example of which for the Pacific is given in Figure 12.

There are wind driven upwellings and geostrophic upwellings, both in coastal areas and in oceanic areas. Coastal upwelling is generated by winds blowing parallel to the shore towards the equator, as in the major upwellings, or is generated geostrophically by the tilt of a current, as in the Somali Current (Stommel and Wooster, 1965). Some areas may include both wind-generated upwellings and geostrophic upwellings, as for example, the Malabar Coast (Darbyshire, 1967). There is a specialized form of upwelling off Cabo Frio in Brazil where warm salty water offshore sinks and is replaced inshore by cooler less salty water and this process is assisted by northeast winds (Emilsson, 1961). Oceanic upwelling includes both the divergences due to the vorticity of the wind stress, all around the subtropical anticyclones, and the geostrophic upwellings within the equatorial system itself, as for example above the Undercurrent and in the domes.

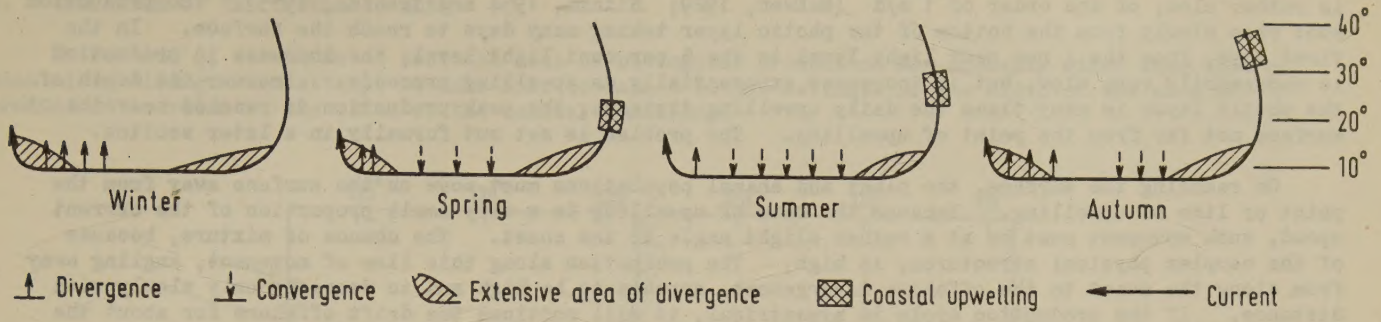

Figure 3. Diagram of the seasonal cycle of upwelling in the eastern boundary currents and in the equatorial system

3. THE BIOLOGICAL BACKGROUND

In the temperate waters of the high latitude cyclones (>45°), the pattern of production cycles is dominated by seasonal changes. Production starts when the critical depth becomes greater than the depth of mixing (Sverdrup, 1953). (The critical depth is that at which production integrated from the surface to that depth equals the integrated respiration.) Subsequently, the rate of production is governed by the ratio of compensation depth (the depth at which the rate of production equals the rate of respiration) to depth of mixing (Cushing, 1962) and therefore is determined by the amount of sunlight, and the strength of the winds and other factors causing mixing, all of which vary seasonally. The upwelling areas in low latitudes are characterized by rather deep photic layers and production increases as the water rises. But, in high latitudes, photic layers are often shallow and so it would be hard to distinguish an effect of upwelling from a normal production cycle.

It is necessary to make this distinction because the cause of high production in subtropical upwelling areas and in the Antarctic is often attributed to the associated presence of nutrients (Hentschel and Wattenberg, 1930; Deacon, 1937). The algal reproductive rate can fall as the nutrients become reduced. Riley (1946), on the basis of an experiment by Ketchum (1939), suggested a level of 0.55 µg-atoms $P.PO_4/l$ to limit algal reproductive rates. The plastic bag experiments in the Pacific of McAllister, Parsons and Strickland (1960) and Antia et al. (1963) show that such a limit must be at a very much lower level, and not only in phosphorus. A production cycle in the North Sea was shown to be completed with little reduction in nitrate, phosphate or silicate, and no reduction in algal reproductive rate (Cushing, 1963; Cushing and Nicholson, 1963) and was thus determined by grazing animals. This does not mean that nutrient lack never limits production, but that its function is that of a fail-safe device in the system, rather than that of a universal limit; in other words, if the grazing animals are absent for one reason or another, production must stop as the nutrients run out. So the very high values of nutrients found in the Antarctic and all over the upwelling areas do not limit the production, nor can they accelerate it. The persistence of production in an upwelling area is due not to the presence of excess nutrient but to persistent addition of living material. There is an argument that production might still be limited by an unnamed nutrient, but it is an infinite regress.

The production cycle in an upwelling area resembles that in temperate waters. The cool water originates from depths of less than 200 m and it contains a resident and sparse population of plants and animals, very like those in temperate waters in early spring. In the photic layer the algae start to divide; as in temperate waters, the increase in animal production is caused by the increase in plant population, and must follow it in time. This delay may be as much as half a generation. It is this delay which allows the production of large stocks of plants, and later, of animals, as in temperate waters. This is in contrast to the deep ocean, where there is no sudden increase in the production rate of plants, so that they do not get out of phase with the animals, and there are low stocks (Cushing, 1959). If mixing were complete and rapid, the new algal production would be eaten by older animals, derived from earlier production, as it upwelled. So if upwelling is to be productive, mixing should be rather a slow process, and since the structures are so readily detected, it is.

If the production cycle in an upwelling area were similar to the temperate one, a bell-shaped curve of production would be expected as a function of distance upwelling similar to the temperate curve as a function of time. At the surface the quantity declines in distance from a maximum at the point of upwelling. The photic layer is usually fairly deep, up to 50 m, and the rate of upwelling

is rather slow, of the order of 1 m/d (McEwen, 1929; Hidaka, 1954 and Yoshida, 1955). So production must rise slowly from the bottom of the photic layer taking many days to reach the surface. In the first days, from the 1 per cent light level to the 5 per cent light level, the increase in production is necessarily very slow, but it increases exponentially as upwelling proceeds. Because the depth of the photic layer is many times the daily upwelling distance, the peak production is reached near the surface not far from the point of upwelling. The problem is set out formally in a later section.

On reaching the surface, the plant and animal populations must move on the surface away from the point or line of upwelling. Because the rate of upwelling is a very small proportion of the current speed, such movement must be at a rather slight angle to the coast. The chance of mixture, because of the complex physical structures, is high. The production along this line of movement, angling away from along the coast to the offshore divergences, appears to be high and to decrease only slowly with distance. If the production cycle is symmetrical, it will continue the drift offshore for about the same period of time as the water takes to rise in the upwelling process. At ½ knot, an upwelling which took 30–50 days to rise through the photic zone might drift 300–600 miles before the decay process was complete.

The coastal upwelling zone is bounded by the offshore divergence at about 100 km. But divergences continue to seaward and the boundary eventually becomes physically imprecise. The boundary in zooplankton (Thrailkill, 1956, 1957, 1959, 1961 and 1963) or surface phosphate phosphorus (California, Department of Fish and Game, 1958) is often far beyond the offshore divergence, perhaps hundreds of kilometres. Because the biological processes have not been examined in detail, the nature of decay process to seaward is not understood. As a convention the limit of the upwelling area is taken as the point where the quantity of zooplankton or phosphate phosphorus is half the maximum from the coast. Zooplankton quantity is used as a convenient index of summed production over a period; phosphate phosphorus is used because it correlates so well with the zooplankton (Holmes, Schaefer and Shimada, 1957).

The positive correlation, first shown by Hentschel and Wattenberg (1930), has been confirmed by Reid (1962b) over the whole Pacific Ocean. If phosphorus is converted to algae, in its turn converted to animal flesh, one might expect an inverse correlation over a time period. If distance from the coast indicates time from the point of upwelling, the inverse correlation should be obvious in the horizontal distributions of phosphorus and zooplankton. When phosphorus is used in the production cycle, it is converted to animal flesh, organic residue (dissolved and particulate) and a stock of algae. So the stock of algae is possibly a transient component in the system (Harvey *et al.*, 1935). The phosphorus in the water at any point, P_R, may be considered as a residue of productive processes, $P_R < P_T$, the initial quantity available for production, i.e. the quantity available at 200 m in an upwelling area. Then, $P_T - P_R = P_U$, the minimum quantity used in production. Strictly we would expect P_U to be directly correlated with Z, the quantity of zooplankton; also, since $P_R = P_T - P_U$ we might expect an inverse correlation between P_R and Z, which is not observed. Let us define P_U in more detail, distinguishing the part of production locked up in the plants, P_p, that absorbed into animal flesh, αP_U and that part which is regenerated by animal grazing, βP_U. Then $P_R = P_T - P_p - \alpha P_U + \beta P_U$. If we then suppose that $\beta P_U > \alpha P_U$ and note that P_p is small compared with P_R, the correlation between P_R and Z is explained. It is not surprising because the turnover rate of phosphorus in lakes was shown to be rapid (Hayes and Coffin, 1951). The same processes probably occur in the sea and Cushing and Nicholson (1963) suggested a turnover rate for phosphorus off the northeast coast of England of perhaps three times a month.

The simplest way of assessing the production in the upwelling areas is to estimate $gC/m^2/d$ from radiocarbon measurements for a region and time period. Koblents-Mishke (1965) has used all the radiocarbon measurements made in the Pacific and has combined the surface observations *in situ* measurements in such a way that all measurements were used. Her chart of primary production in the Pacific is unique and includes measurements made in upwelling areas and along the equator. Observations have been made elsewhere, off South Africa (Steemann Nielsen and Jensen, 1957), off East Africa and Arabia (Ryther *et al.*, 1967), and in the eastern Indian Ocean (Angot, 1961), all in upwelling areas. Such observations will be averaged.

For physical and biological reasons, the biology of upwelling areas will be studied in the subtropical anticyclones. The cycle of production in an upwelling area is considered essentially as a temperate cycle rising slowly from the bottom of a fairly deep photic layer. Because of a slow and continuous mixture, with continuous addition of living material at the coast and offshore, the distribution of biomass in an upwelling area is fairly uniform, in so far as biological systems can be uniform. Because divergences continue far offshore beyond the boundary at 100 km, the width of the upwelling area biologically is considered to extend beyond the obvious physical boundaries. The width will be estimated from zooplankton and phosphorus distributions, which are correlated, an explanation for which is given. Then within each area and season primary and secondary production will be estimated for a number of upwelling areas.

4. THE WIDTH OF THE UPWELLING ZONE

In section 3, it was noted that the zone of biological production was probably wider than that of coastal upwelling. An attempt is made here to make a better estimate of the width of the zone of production as ratio to the width of the coastal upwelling.

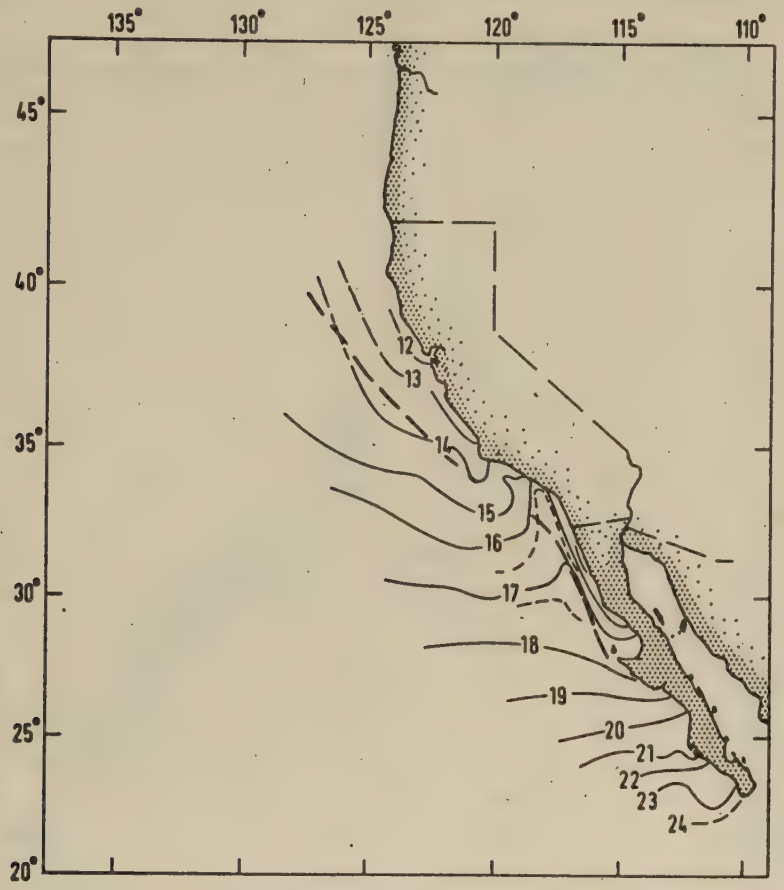

Figure 4. Mean temperature off California at 10 m for the years 1950-62, Lynn (1967); the heavy broken line was drawn by eye where the isotherms lie parallel to the coast

The thirteen-year mean temperatures at 10 m off California and Baja California, from 1950 to 1962, are shown in Figure 4, (Lynn, 1967). Because of the intense sampling in the area as part of the Calcofi programme, the distributions are well established. The physical boundary to the coastal upwelling has been drawn by eye where the isotherms tend to run parallel to the coast. From Baja California to Point Conception, the boundary is about 100 km offshore, but from Point Conception to Cape Mendocino it may be nearer 200 km. Lynn has examined the same data in much more detail. All the temperature data were fitted to a harmonic regression by date. The high correlation of temperature with date shows the stable areas, whereas upwelling is shown by low correlation coefficients.

Figure 5 shows the distribution of correlation coefficients and the line has been drawn by following the poor coefficients (using r < .75 as a criterion) at roughly 100 km offshore. Another way of showing the upwelling areas is given in Figure 6, showing the months of occurrence of minima in temperature on the fitted regression curves, the figure shows the average position of upwelling by months. The areas shown are much closer to the biological boundaries and perhaps they indicate the direction of drift offshore from the coast.

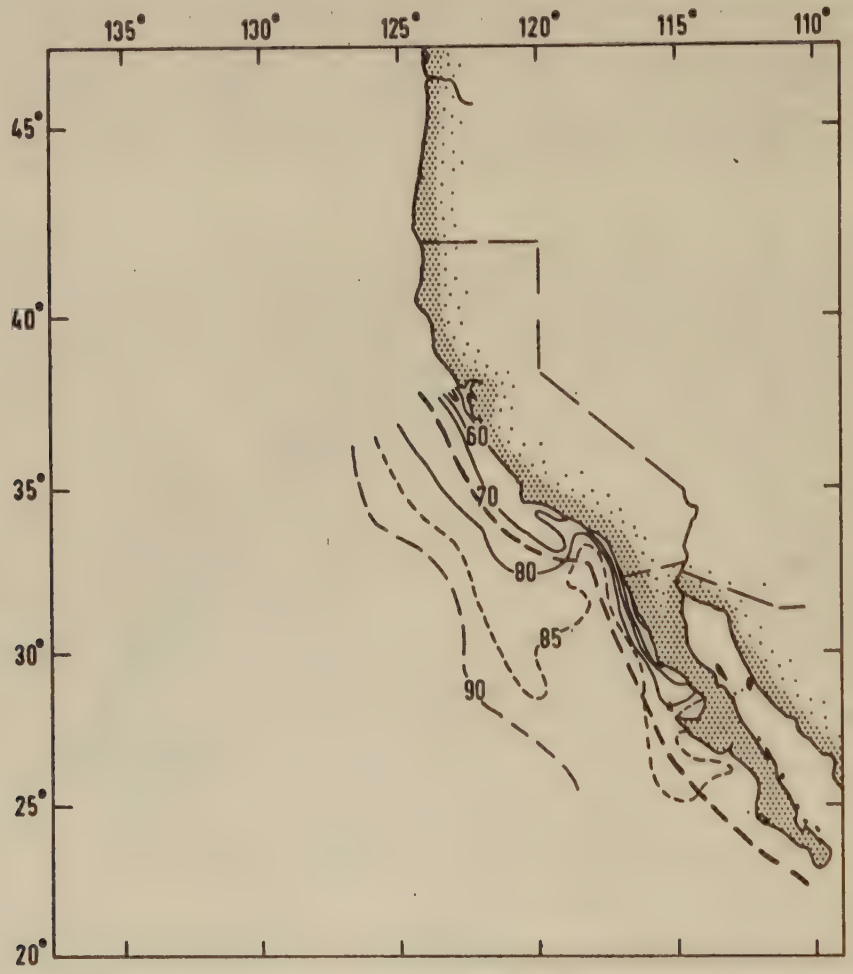

Figure 5. Distribution of correlation coefficients of temperature on date at positions off California fitted to a harmonic regression (Lynn, 1967). The heavy broken line was drawn by eye using the coefficient of determination

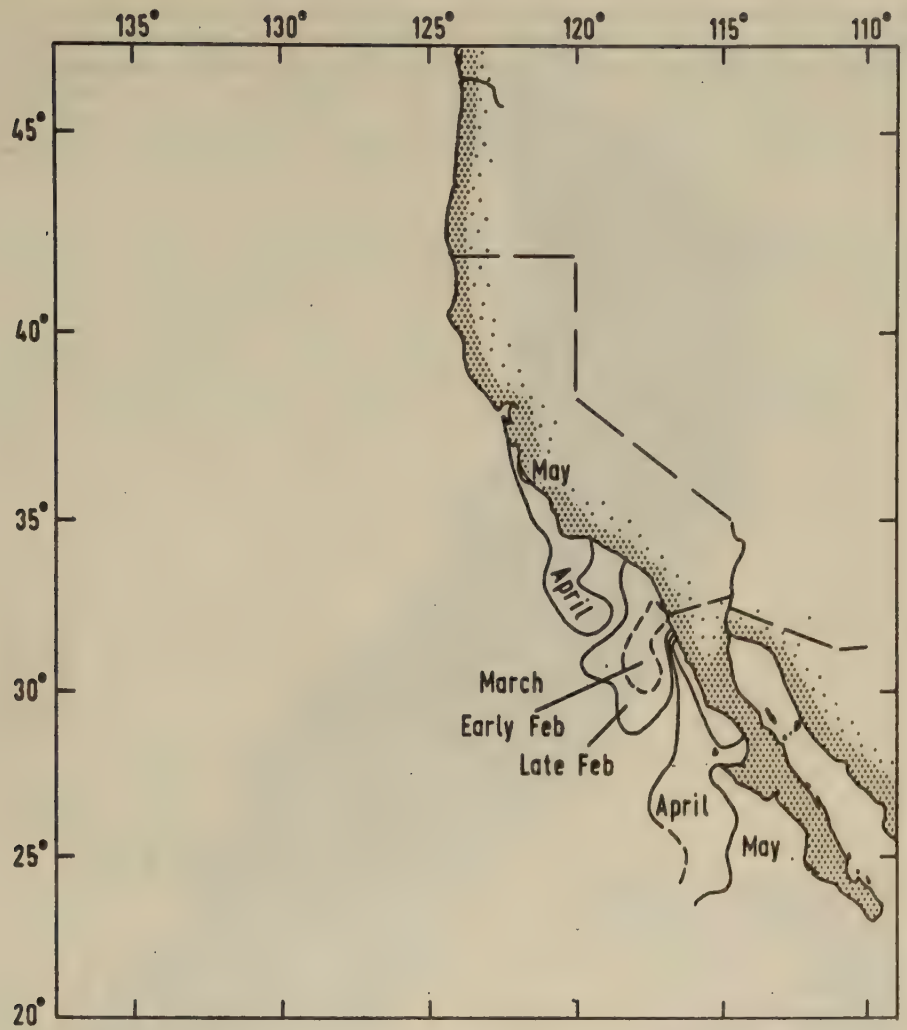

Figure 6. Months of occurrence of the minima of the harmonic regression of temperature on date off California (Lynn, 1967).

The width of the production zone can be examined in the zooplankton distributions off California from 1950–1959 (Thrailkill, 1956, 1957, 1959, 1961 and 1963). A typical distribution is given in Figure 7; the broken line is drawn at a median density. The width of the zooplankton zone was tabulated by year and area and averaged for the ten years, ranging from 200–500 km. When the estimates from the temperature distributions are compared with those from the distributions of zooplankton, the ratio - width of productive zone to width of physical upwelling - is 2.5. To treat all upwelling areas in the same way, the width is estimated from surface temperature distributions, like that in Figure 5, and is raised by 2.5.

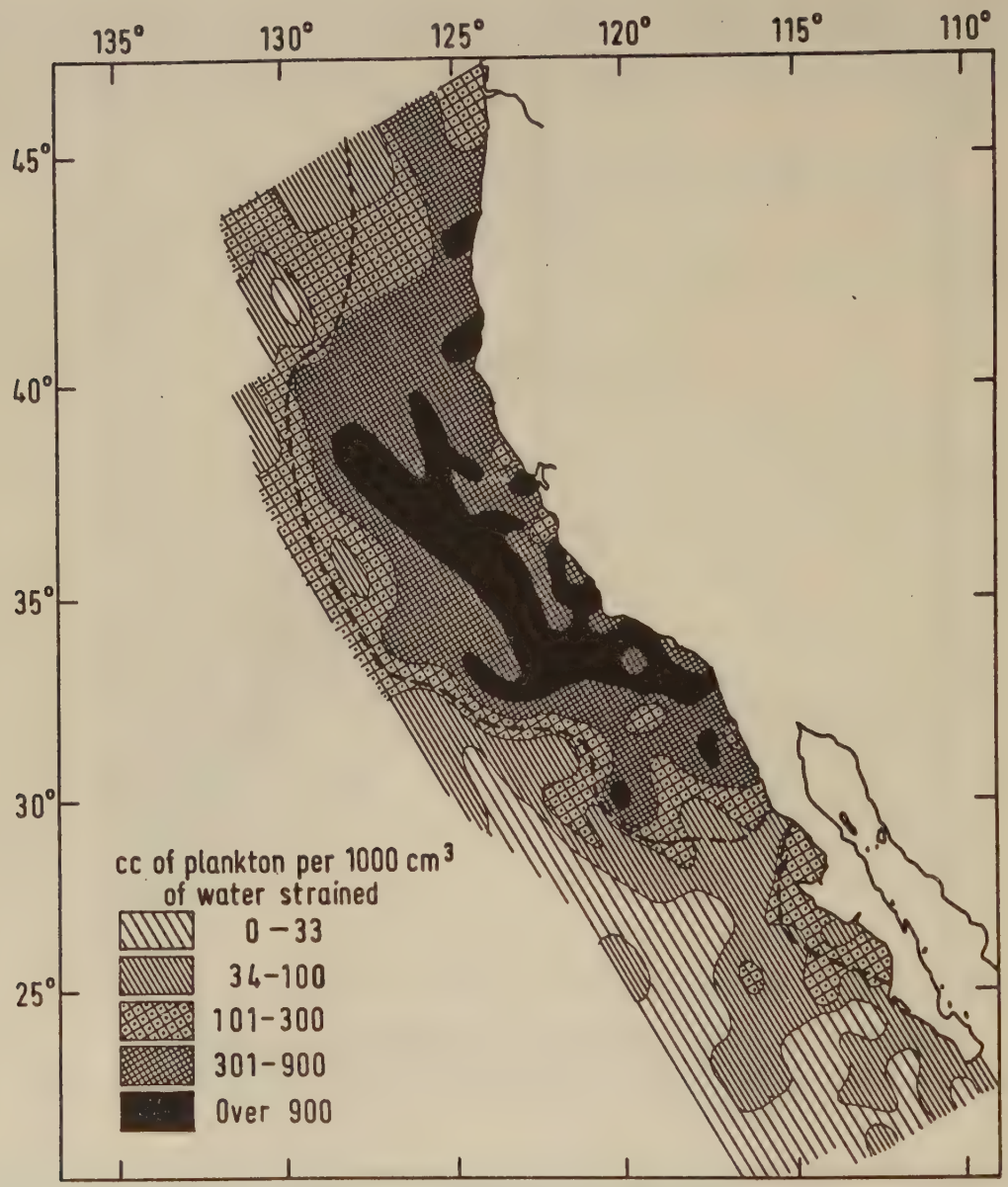

Figure 7. A typical distribution of zooplankton off California (Thrailkill, 1956); the broken line is drawn at a median density

5. THE RELATION BETWEEN PRODUCTION AND RATE OF UPWELLING

The ascending velocity in upwelling, W_h, can be estimated in a number of ways, but because it is low, 0.1-3.0 m/d (McEwen, 1929; Yoshida, 1955; Hidaka, 1954; Posner, 1957; Wyrtki, 1964) no direct measurements are available. Wooster and Reid (1963) show that the Ekman transport off northern Peru in winter is the greatest of all the upwelling areas. It might follow, therefore, that the production in northern Peru in winter was the greatest. However, the quantities of carbon and zooplankton are no greater there than in other upwelling areas (see Table I); indeed, the data show the quantity of production to be less in northern Peru than in other major upwelling areas.

The simplest view of the upwelling production cycle is to consider it as starting at the bottom of the photic layer and continuing as the water rises. As production starts from low quantities, the cycle in the upwelling area resembles the temperate cycle rather closely. Heinrich (1961) suggests a generation time for the zooplankton in the upwelling areas of about 40 days, so effective grazing should start about 20 days after the start of upwelling. So the peak of the production cycle should occur at or near the surface, at or near the line of upwelling. A more complex case occurs if the plant production becomes vulnerable by mixture to zooplankton arising from earlier production. Jones and Folkard (1968), in their sections of the Canary Current, show distributions of physical properties which might bring the vertically migrating zooplankton inshore towards the line of upwelling.

Let us consider production in the rising water, without grazing. From Steele and Menzel (1962),

$$p = \alpha I_o e^{-kZ-2e^{-kZ}} \qquad \ldots\ldots (1)$$

where I_o is the average radiation at the surface in g cal/cm^2/d (Steele and Menzel's figure of 180 g cal/cm^2/d for the Sargasso Sea has been used);

Z is depth in m;
k is the extinction coefficient (the value k = 0.1 has been used, ignoring its possible increase with increasing production);

α is a constant (=0.48);
p is the daily production in gc/m^3/d.

Let Z_p be the depth of the photic zone, hence

$$Z = Z_p - W_h t \qquad \ldots\ldots (2)$$

where W_h is the ascending velocity in m/d.

Between time t and t + δt,

$$p_{\delta t} = \alpha I_o e^{-(k(Z_p - W_h t) + 2e^{-k(Z_p - W_h t)})} \delta t \qquad \ldots\ldots (3)$$

then the total production, in gC/m^2/d, as water upwells from the bottom of the photic layer ($Z = Z_p$, $t = 0$) to the surface ($Z = 0$, $t = Z_p/W_h$) is

$$p_{total} = \int_{t=0}^{Z_p/W_h} \alpha I_o e^{-(k(Z_p - W_h t) + 2e^{-k(Z_p - W_h t)})} dt \qquad \ldots\ldots (4)$$

$$= \frac{\alpha I_o}{-2kW_h} \; e^{-2e^{-k(Z_p - W_h t)}} \Big|_0^{Z_p/W_h}$$

$$= \frac{\alpha I_o}{2kW_h} \left(e^{-2e^{-kZ_p}} - e^{-2}\right) \qquad \ldots\ldots (5)$$

I am grateful to my colleague, Mr. J.G.K. Harris, for the development of equations (2) to (5).

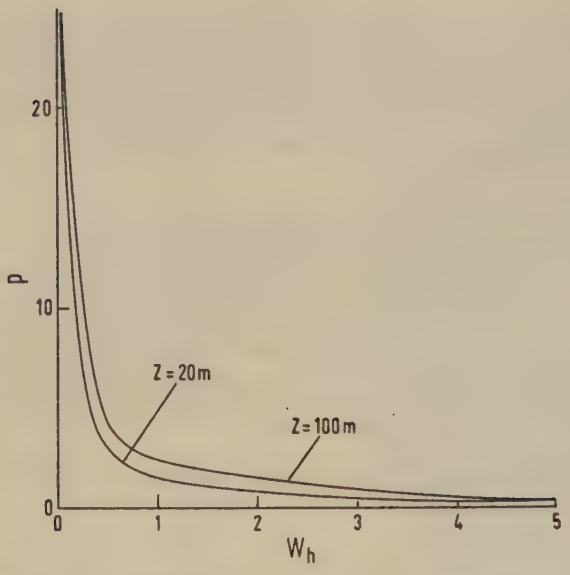

Figure 8. Relation between total production, p, during ascent and ascending velocity, W_h, (in m) for a range of depths of the photic layer.

Figure 8 shows the relation between total production during ascent (for two depths of photic layer) and ascending velocity. Ignoring grazing the slower the ascending velocity, the greater the production during the ascent, irrespective of the depth of the photic layer. Let grazing become effective after 20 days. Then with a photic layer 20m deep, grazing starts at the surface with an upwelling of 1 m/d, and if it is 100 m deep it starts at the surface with an upwelling of 5 m/d. So the upwelling production cycle, well grazed, can reach a peak at the line of upwelling at the surface. It is obvious from Figure 8 that an upwelling velocity of <0.5 m/d will give the production generating its own grazing capacity at the surface. A greater upwelling velocity, irrespective of the depth of the photic layer, means that the production has not gone on for very long (less than half a generation time), when it reaches the surface and may become vulnerable to the greater grazing capacity of other animal populations. Perhaps the faster rate of upwelling off Peru modifies the production cycle in this way, leading to rather lower standing crops than expected.

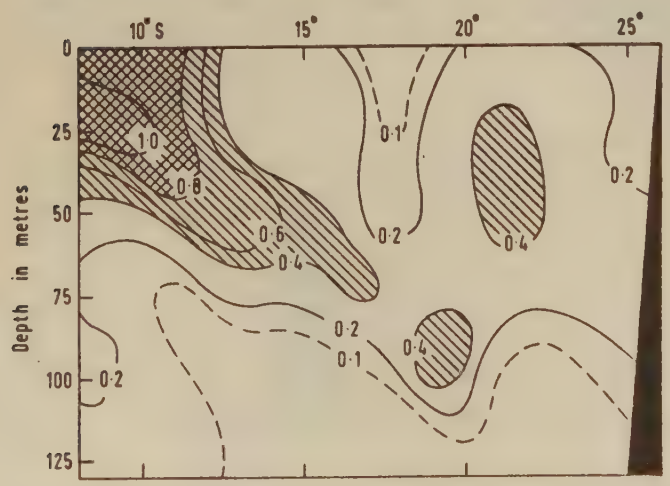

Figure 9. A vertical section of carbon production in mg $C/m^3/d$, off Java during the period of upwelling (Japan, Science Council. National Committee for IIOE, 1966)

Figure 9 shows a vertical section of carbon production (Japan, Science Council. National Committee for IIOE, 1966) from Java to Western Australia during the period of upwelling off Java. It is a section of a dynamic process, but we may imagine the upwelling entraining northwards and slowly increasing its production as it rises. It is not confirmation of the process imagined above, but an illustration of how such a system might work. A series of sections (like that in Figure 9), closely spaced in time, and on a smaller horizontal scale could be used to analyze the production cycle in an upwelling area and even estimate the rate of upwelling.

6. DESCRIPTION OF AREAS

In this section the upwelling areas are examined in more detail. The first subsection covers the main areas of upwelling in the eastern boundary currents. The second examines the equatorial systems. The domes are treated in the third. In the fourth are grouped all the upwellings in the Indian Ocean and Indonesian area, because they are dominated by the monsoon system.

The U.S. Navy Hydrographic Office Publication 225 (1944), the World Atlas of Sea Surface Temperatures, gives charts by months. From them each upwelling area can be identified, and its length and width for each season can be estimated. For each area relevant publications are also used, but the main reliance on the U.S. Navy Hydrographic Office Publication 225 ensures that the upwelling areas are all treated in the same way. Atlases of wind strength and direction were also used, particularly to pinpoint the peak season and its position (U.K. Meteorological Office, Air Ministry, 1957).

6.1 The main areas

There are four main upwelling areas – on the west coasts of North and South America and of North and South Africa. There should be one off the west coast of Australia, but it appears to be limited to the northwest coast for a short period. In Table I the four main areas are split into sub-areas by seasons. The length of each is given from the published data. The width of the productive strip is defined above.

MAIN UPWELLINGS

West coast of North America

California Current

		Season(a)	Length (km)	Width (km)	Area (km^2)
1.	Baja California to Point Conception	FMAMJJ	880	190	169.10^3
2.	Point Conception to Cape Mendocino	AMJJAS	560	190	106.10^3
3.	Cape Mendocino to Cape Flattery	MJJASO	800	290	230.10^3

In addition to the U.S. Navy Hydrographic Office Publication 225, full descriptions of the California Current are given in Sverdrup (1938), Yoshida (1955), Reid, Roden and Wyllie (1958), Wooster and Reid (1963), Stefansson and Richards (1964) and in the California, Department of Fish and Game Progress Reports 1953 and 1958. The countercurrent below 200 m, the inshore current, the northward seasonal shift, the generation of large swirls and the intermittent character of upwelling are all described in these papers.

West coast of South America

Peru Current

		Season	Length (km)	Width (km)	Area (km^2)
1.	Cape Blanco to 10°S	FMAMJJASO	720	400	288.10^3
2.	10°S to Arica	FMAMJJASO	1300	170	191.10^3
3.	Antofagasta to Cape Carranza	DJFMAMJJ	1500	250	375.10^3
4.	Cape Carranza to 45°S	ASONDJFM	1000	150	150.10^3

The first full description of the upwelling system off South America was given in Gunther (1963); here the countercurrent below 200 m and the inshore countercurrent were described, together with the seasonal and coastal patterns of upwelling. Posner (1957) described the phenomenon known as El Niño and made some estimates of ascending velocity. Schaefer, Bishop and Howard (1958) showed that the zone of biological production extended far to seaward particularly in the Peru oceanic current. Bjerknes (1961) in his

Note (a) Underlining donates the main season

study of the El Niño phenomenon described the whole system including the equatorial divergences. Wyrtki (1966) summarized much of the data and generalized the current structure.

Wooster and Reid (1963), from their Ekman transport values normal to the coast, showed that the winter upwelling off Peru was the most intense. This is borne out by the wind distributions, the wind blowing parallel to the coast at this time. But, as will be shown below, the production at this time is not the heaviest. From Gunther's work and from Wooster and Reid, there appears to be a break in the upwelling system between Southern Peru and Antofagasta in Chile. This may be an effect of the changed angle of the wind to the coastline.

West coast of North Africa

Canaries Current

		Season	Length (km)	Width (km)	Area (km^2)
1.	Freetown to Dakar	ONDJF	800	50	40.10^3
2.	Dakar to Cap Blanc	ONDJFMA	700	150	105.10^3
3.	Cap Blanc to Canaries	AMJJAS	1020	300	306.10^3
4.	Canaries to Casablanca	AMJJAS	1000	150	150.10^3
5.	Cap St. Vincent to Vigo	JJASO	600	150	90.10^3

The Canary upwelling is not so well known. The charts of surface temperature (U.S. Navy Hydrographic Office Publication 225) are reinforced by the work of Furnestin (1959) between Cap Jubi and north of Casablanca. Quarterly cruises and a few sections show upwelling to some extent in the whole area in summer, but concentrated between Cap Ghir and Mazagan. A further upwelling appears late, north of Casablanca. The region between Freetown and Dakar has been examined by Berrit (1958, 1961, 1962) who shows the shift with season from Cap Vergas northwards as winter gives way to spring. Jones and Folkard (1968) have published sections of the whole current, showing the upwelling zone to be limited to the upper 200 m. A remarkable point from their sections is the obviously slow rate of mixture in various properties, the upwelling tongue bending downwards to seaward.

West coast of South Africa

Benguela Current

		Season	Length (km)	Width (km)	Area (km^2)
1.	Pointe Noire to Porto Amboin	FMA	700	50	35.10^3
2.	Baia dos Tigros to Walvis Bay	DJFMAMJJ	800	300	240.10^3
3.	Walvis Bay to Orange River	SONDJFMAMJJA	700	300	210.10^3
4.	Orange River to Cape of Good Hope	SONDJFMA	700	220	144.10^3

The upwelling area in the Benguela Current was first described fully by Defant (1936). Hart and Currie (1960) published the first specific work on upwelling. They showed the seasonal shift southward, which can be linked with the winter upwelling much further north between Point Noire and Amboin (Figure 14) (Berritt, 1961, 1962). They also suggested that a countercurrent was present and described the "roller bearing" of convergence and divergence about 100 km offshore. The season and length of the upwelling area is taken from the U.S.Navy Hydrographic Office Publication 225. Darbyshire (1953) and Buys (1959) have given charts of surface temperature also and Darbyshire described the system of upwelling. Copenhagen (1953) showed where the points of upwelling were along the coast between Cabo Frio and the Orange River, together with some points off Cape Province. In general it is a long persistent upwelling in the centre, shorter to the south and to the north. The seasonal cycle, although present, is rather hard to distinguish because of the long persistence in the central region.

6.2 The equatorial system

At the equator the north and south equatorial gyres meet, forming a westbound North Equatorial Current (at 10°-20°N in the Pacific) and westbound South Equatorial Current (at 5°N to 10°S in the Pacific). Between the two equatorial currents runs an eastbound Equatorial Countercurrent (at 5°-10°N in the Pacific), the strength of which varies with season. In the Pacific the seasonal strengths are:

	North Equatorial Current	Countercurrent	South Equatorial Current
September to January	weak	weak	strong
February to April	strong	None	weak
May to July	strong	strong	weak
July, August	weak	strong	strong

(Knauss, 1963)

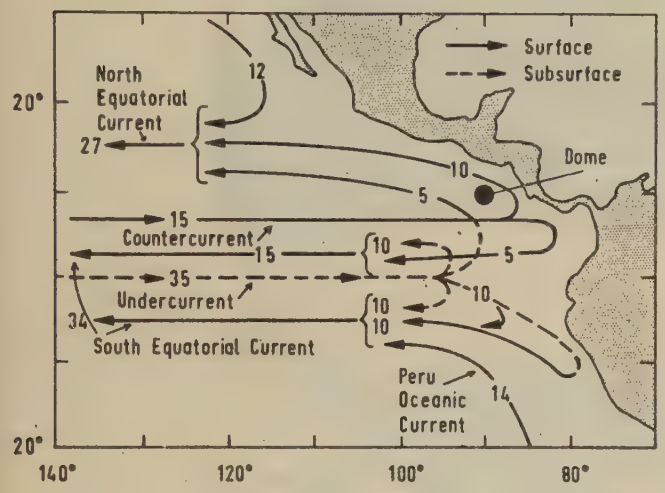

Figure 10. Currents in the Eastern Tropical Pacific during the period June to December (Wyrtki, 1966); the figures represent transports in $cm^3 10^{12}$/sec

At the equator beneath the South Equatorial Current runs the eastbound undercurrent, or Cromwell Current, which originates roughly in mid-ocean. In the western ocean two undercurrents may appear beneath the two equatorial currents (for example the Lomonosov Current under the South Atlantic Equatorial current). Figure 10 shows how the currents are resolved in the eastern tropical Pacific (Wyrtki, 1966); notable is the great width of the system and the structural connection to the California and Peru Currents. There is an area of offshore divergence spreading from the upwelling areas to the equatorial currents. The Peru Oceanic Current is a good example of this effect (Wyrtki, 1966). In the equatorial complex shown in Figure 10, the two equatorial currents tend to generate divergences and the countercurrent convergences.

Beneath the Cromwell Undercurrent, at the equator, radiolarian skeletons are deposited in relatively dense quantities (Arrhenius, 1963). There is a productive zone, narrowly confined to the region of the Undercurrent, which is more productive than the divergences of the South Equatorial Current near the equator. The same point is made in Figure 15 showing the distribution of radiocarbon observations, a narrow productive band at the equator in the eastern ocean above the Cromwell Undercurrent.

Figure 11 shows the distribution of zooplankton in the upper 150 m in the Pacific (Reid, 1962b). Not only are the divergences round both subtropical gyres well shown, but both coastal upwelling areas off California and off Peru. But more remarkable is the wide band of zooplankton at the equator; the eastern dense patches coincide with zones of divergence in the South Equatorial Current and the North Equatorial Current. A similar picture of phosphorus at the surface shows an eastern distribution centred about the undercurrent and its connection with the Peru Current. That of phosphorus at 100 m shows the distribution of the North and South Equatorial Currents with the barren Countercurrent between them. Between the Countercurrent and the North Equatorial Current lies a zone of convergence in the northern summer.

Figure 12 gives the distribution of divergence and convergence in the Pacific in the northern winter and the northern summer. There are extensive areas of divergence in both seasons at the roots of the North Equatorial and South Equatorial Currents. In the northern summer there is convergence all along the Countercurrent, with intermittent divergences along the South Equatorial Current. In the northern winter there are divergences where the Countercurrent is weak or non-existent, particularly in the eastern part of the ocean.

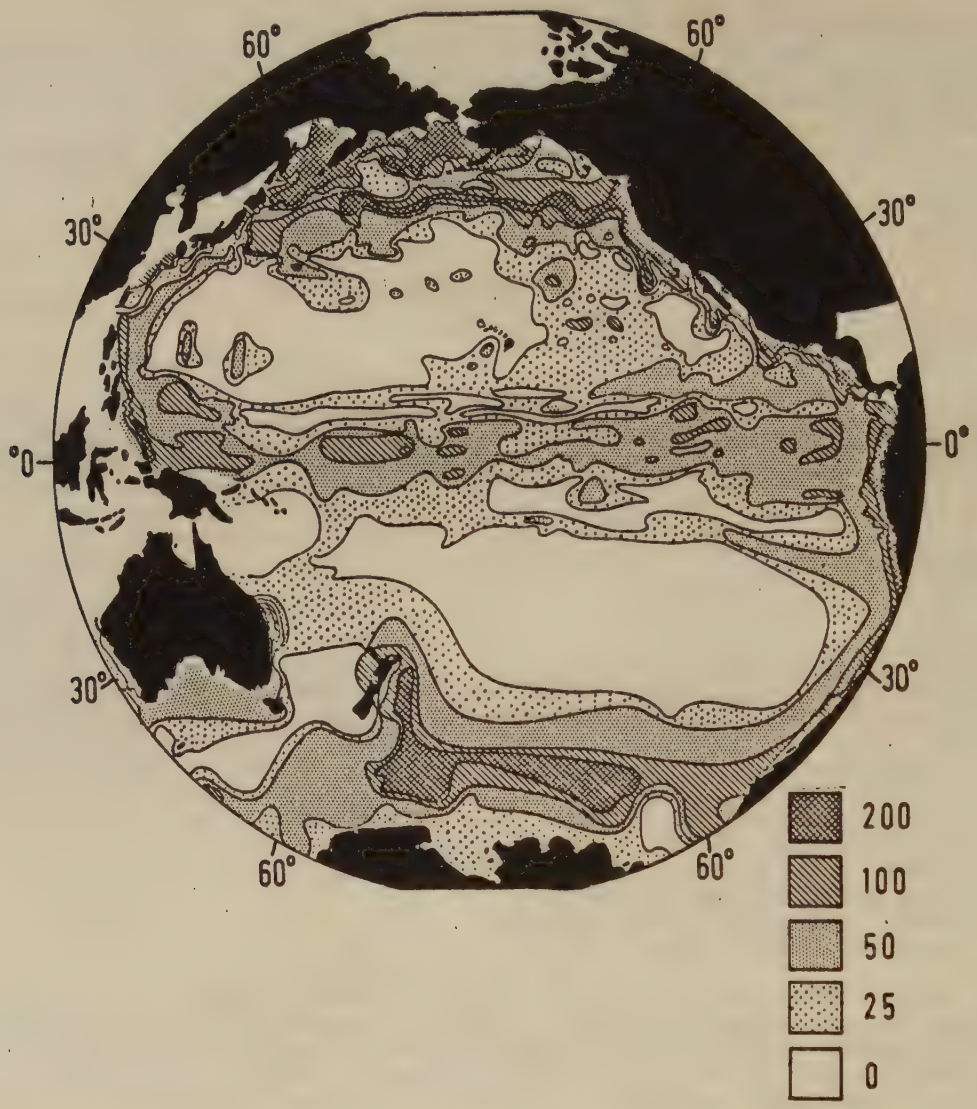

Figure 11. Distribution of zooplankton in the upper layers of the Pacific, in ml/1000 m^3 displacement volume (adapted from Reid, 1962b)

Areas of divergence are difficult to define in such a complex system and so no detailed estimate has been made. However, the area of the equatorial system is large, 10° wide (across the equator), and excluding the Countercurrent, 115° long in the Pacific, 50° in the Atlantic and 50° in the Indian Ocean. The high season of divergence is in the northern summer in the North Equatorial Current and in the southern summer in the South Equatorial Current, six months for the whole area.

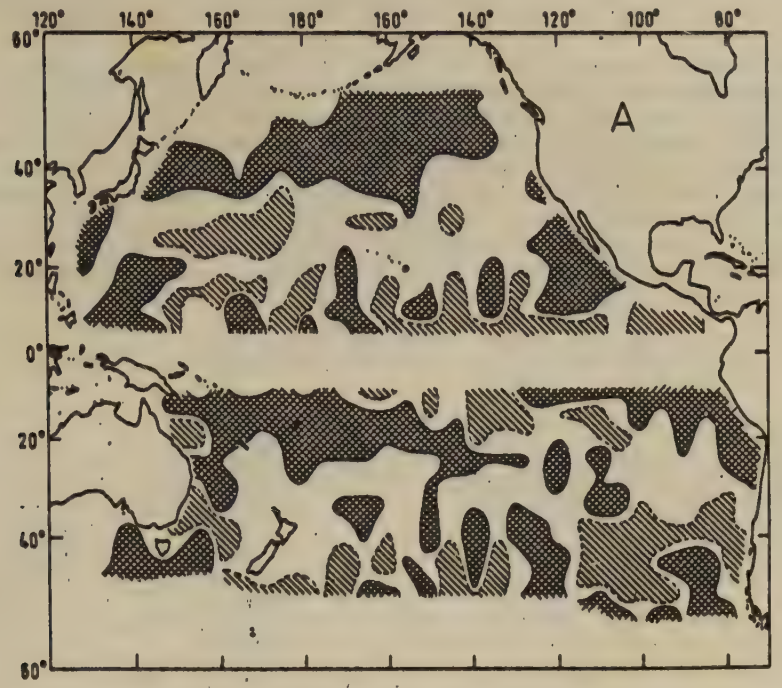

Figure 12(a)

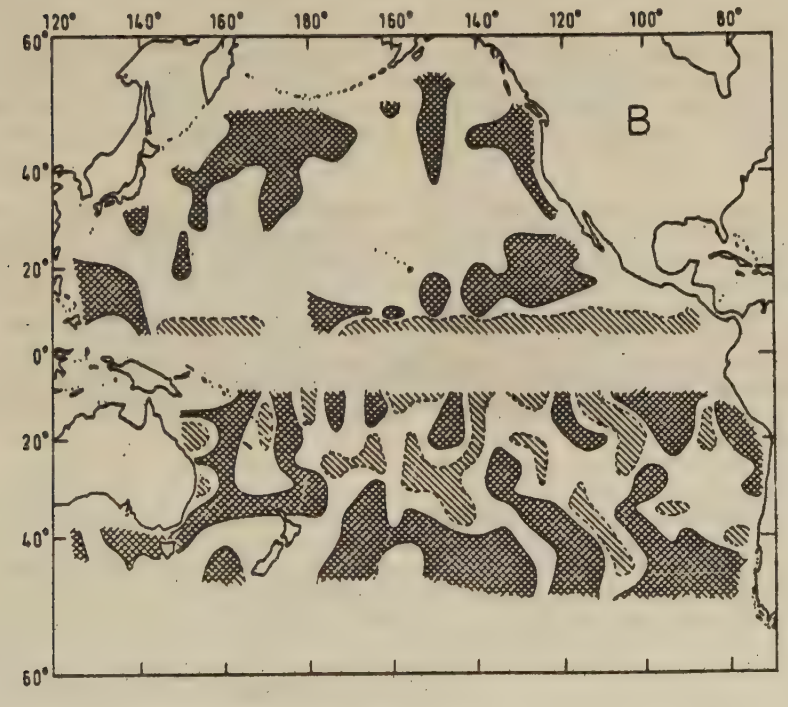

Figure 12(b)

Figure 12. Distributions of divergence and convergence, in $kg/m^3/sec$,
(a) in the northern winter
(b) in the northern summer
(after Hidaka and Ogawa, 1958); the cross-hatched areas are divergences and the diagonally shaded ones are convergences

6.3 Domes

The classic dome is the Costa Rica Dome at 7.5-9.0°N, 87-90°W (Wyrtki, 1964). It is most prominent when the Equatorial Countercurrent is strongest, in late summer and in autumn but it exists at all seasons, even in February and March when the Countercurrent appears to be absent. The Countercurrent turns north into the Costa Rican Coastal Current and then westward into the North Equatorial Current. The eddy gives rise to the dome and with the fluctuations in current strength, the shape changes and domelets may become split off. Figure 13 shows a section of the dome, in phosphorus (Cromwell, 1958). Upwelling is generated on the left flank of the anticyclonic flow and by a lateral transport across the dome (Wyrtki, 1964). Consequently there must be a sinking on the right of the flow, shown most prominently in a hollow south of the dome, as part of the Countercurrent turns south and then west into the South Equatorial Current.

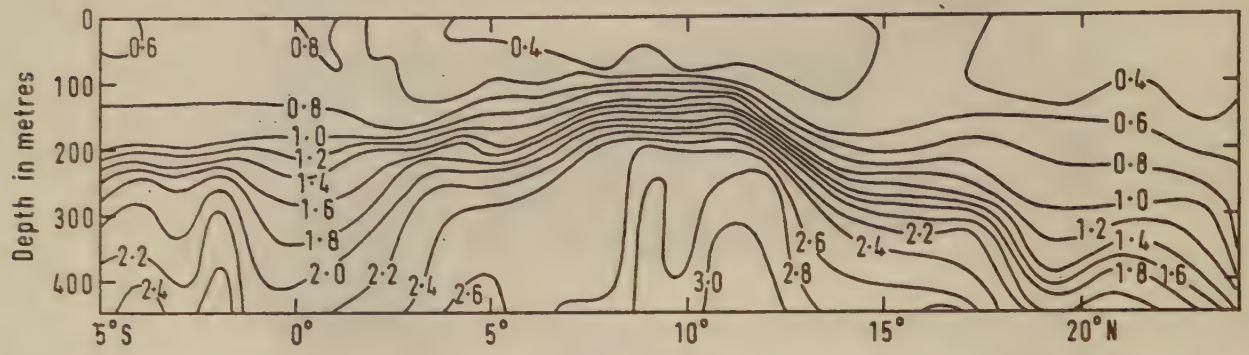

Figure 13. Section of the Costa Rica Dome, in phosphorus (µg-atoms/l), (Cromwell, 1958)

Wyrtki(1962) has shown that the upwelling off Java and Sumbawa is a dome analogous to the Costa Rica Dome; there is an Indian Ocean Countercurrent, but it is more temporary than the Pacific one, because of the switch from one monsoon to the other. The dome off Java and Sumbawa lasts only from May to September during the southeast monsoon (a name given to the southeast trades in the Indonesian area).

In the eastern tropical Atlantic the domes are described by Mazeika (1967). From January to April, in the southern summer there is a dome off Angola, the Angola Dome. Similarly from July to September, in the northern summer, there is a dome southwest of Dakar, the Guinea Dome. It is formed as the Equatorial Countercurrent turns into the North Equatorial Current; in other words, it is an exact analogue of the Costa Rica Dome but is seasonal like the Sumbawa Dome presumably because the Equatorial Countercurrent in the Atlantic is less strong than that in the Pacific. The Angola Dome cannot be formed in the same way but it has a cyclonic circulation; perhaps it is generated by the turning of the Undercurrent into the South Equatorial Current.

Mazeika also shows that there is a dome just south of the equator between 8°W and 3°E, which is a divergence generated by the easterly winds offshore from the upwelling area off Ghana and the Ivory Coast. Here there is a main period of upwelling from June to November between Cape Palmas and Cotonou; there is a temporary and local upwelling between the Sassandra River and Abidjan. It is associated with west south west winds parallel to the coasts from Cape Palmas and Cape Three Points (Berrit, 1961, 1962). Figure 14 shows the appearance of the Guinea upwelling by time and coastal position, as indicated by temperature differences; the interesting point is the connection between the main upwellings, the Canary and Benguela. That in the Benguela is really the Pointe Noire extension, when the Angola Dome is absent much of the Benguela Current itself having turned westward at a higher latitude into the South Equatorial Current. Similarly, the Canary Current upwelling is present south of Dakar when the Guinea Dome is absent.

The area of the Costa Rica Dome is $1.5.10^5 km^2$. That off Java is given as $3.10^5 km^2$, taken from Wyrtki (1964). The Angola and Guinea Domes are possibly a little larger than that off Java. The area of the Guinea upwelling is set provisionally as $1.10^5 km^2$, from the length of coastline (10°) and a distance offshore of 160 km (from the U.S.Navy Hydrographic Office Publication 225.

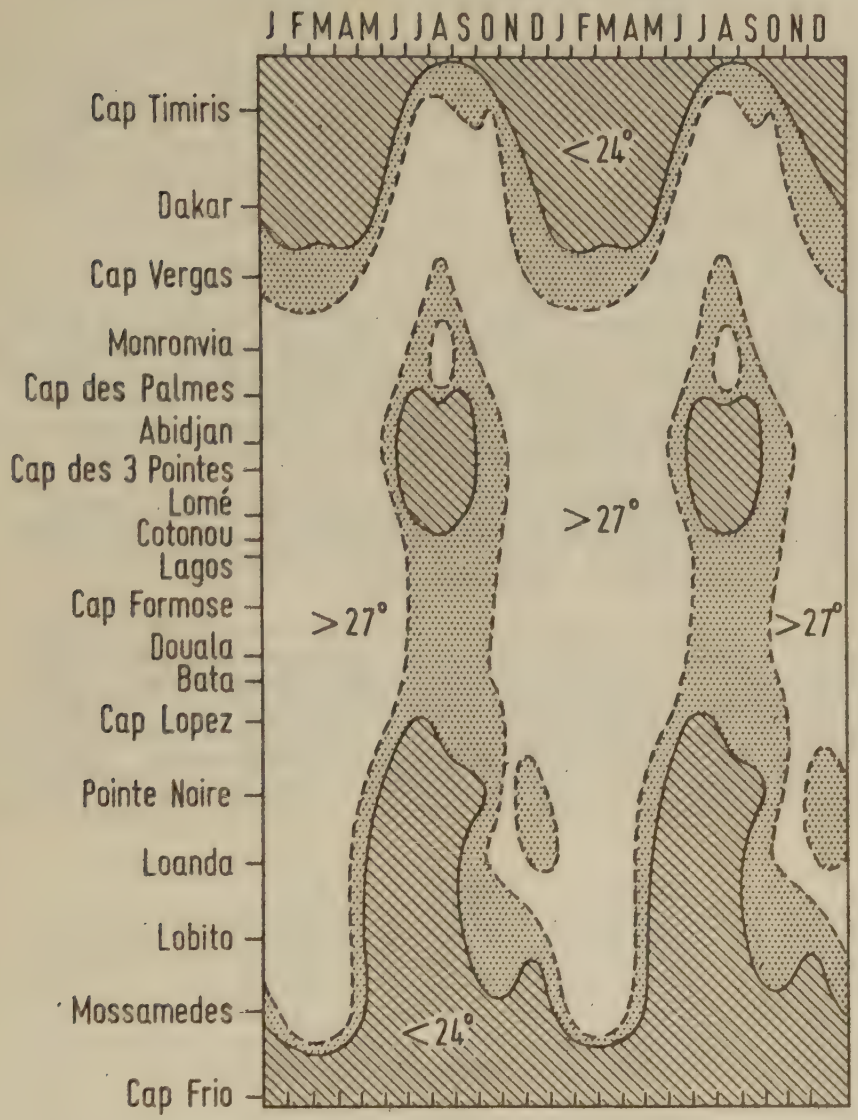

Figure 14. The timing and position of upwelling in the Guinea Current and in relation to the Canary and Benguela Currents (Berrit, 1962)

6.4 Upwellings in the Indian Ocean and Indonesian region, including the South China Sea

There are a number of upwellings associated with the southwest monsoon, which blows from April to September. They are in the Somali Current, off southwest Arabia, and off the Malabar coast of India. That in the Somali Current is a geostrophic upwelling caused by the tilt in the thermal structure as the Current swings eastward away from the Horn of Africa (Warren, Stommel and Swallow, 1966; Swallow and Bruce, 1966). It is associated with the southwest monsoon only in the sense that the current flows during the period of the monsoon. Being a western boundary current it is associated with wind stress over the whole ocean as well as locally. The upwelling is limited to an area between Cape Guardafui, the eastern end of Socotra Island, 9.5°N, 54.5°E (in the latitude of Ras Mabber), and a point on the Somali coast which shifts with season. It is possible that the biological effects of the upwelling drift seawards in the swift current (Ryther et al., 1966). The areas of upwelling are roughly as follows, with season:-

	Distance to Cape Guardafui (km)	Area (km^2)
May	375	94×10^3
June	625	112×10^3
July	625	112×10^3
August	375	94×10^3
September	375	94×10^3
October	200	61×10^3

The sea surface temperature distributions by months are given in the U.S. Navy Hydrographic Office Publication 225. Further particular distributions are given by Swallow and Bruce (1966), Warren, Stommel and Swallow (1966), Stommel and Wooster (1965) and Foxton (1965). All the data are summarized for wind, surface temperature and salinity, nutrients and some biological observations in Wooster, Schaefer and Robinson (1967) for the northwest Indian Ocean. From the latter observations the southern boundary on the Somali coast was chartered by months, which explains the differences in area in the table above.

The work of Ryther et al. (1966) shows high carbon production in a wedge northwest of Madagascar and some patches on the African coast at the southern end of the Mozambique channel. The wedge northwest of Madagascar is presumably related to the divergence between the Somali and Agulhas currents (Ivanenkov and Gubin, 1960) as they split away from the two equatorial currents.

Off southwest Arabia there is a coastal upwelling induced by the southwest monsoon. The oceanographic data given in Wooster, Schaefer and Robinson (1967) show that upwelling ceases at the entrance of the Persian Gulf, but suggests a slight effect on the coasts of Baluchistan during the same period. This is supported by the work on primary productivity in the area during the Indian Ocean Expedition by the Anton Bruun (Ryther et al., 1966) showing intense production spreading across the Arabian Sea to the coasts off Pakistan. The cruise on H.M.S. OWEN shows upwelling and phytoplankton production in April and May off Karachi (Lee, 1963). The same survey shows a biological boundary much further to seaward than suggested by the oceanographic data quoted above, as might be expected. The areas are from Wooster, Schaefer and Robinson (1967):-

		Length (km)	Width (km)	Area (km^2)
May	As Salala - Ras al Hadd	720	175	126×10^3
June	As Salala - Ras al Hadd	720	175	126×10^3
July	Ras Fartak - Ras al Hadd	920	175	161×10^3
August	Mukalla - Ras al Hadd	1240	175	217×10^3
September	As Salala - Ras al Hadd	720	150	126×10^3
October	Marbat - Al Khalaf	430	75	32×10^3

During the southwest monsoon a southerly current is generated, with a thermocline tilt along the Malabar coast of India. The upwelling is very shallow, originating from perhaps 20 m (Darbyshire, 1967), but the surface water is as a consequence 6°C cooler. During July to October, low salinity water spreads over the surface from the rivers and it is at this period that the peak algal production occurs (Subramanyan and Sarma, 1965). During September and October, the post-monsoon period, there is a true wind-induced upwelling between Alleppey and Guilon, off Cochin, and a countercurrent is developed at 75-100 m (Rama Sastry and Myrland, 1959). The situation off the Malabar coast is complex and probably the production is quite high, as indicated by the presence of phosphatic deposits offshore (Tooms, 1967; see Figure 19). It is clear that upwelling extends from Trivandrum as far north as Panjim, but because of its nature and shallow origin reliable areas of upwelling cannot be estimated with the methods used in the other areas. It is possible that the extent of phosphatic deposits indicate the region of upwelling as well as any other method at the moment.

Banse (1968) has examined the upwelling system along the whole coast and shows that an oxygen deficiency can occur below the thermocline during the upwelling period; indeed catches of demersal fishes are reduced in zones of low oxygen tension (<2 ml/l).

In the Bay of Bengal upwelling has been detected off Walthair in February and March (LaFond, 1954); it probably extends up the coast to Sangor Island in June. Ganaparti and Murthy (1954) have described the circulation during this period in the Bay of Bengal. Under the southwest monsoon, upwelling probably occurs all along the coast of Orissa, parallel to the monsoon. The work of LaFond (1957) has shown a long coast of upwelling. An area has been estimated for this coast, based on the length of coastline and a distance of 200 km offshore.

Between December and February upwelling occurs in the Andaman Sea (LaFond, 1957; Wyrtki, 1961) in a rather limited area on the coast of Burma opposite the Andaman Islands. Upwelling also occurs in the shallow Gulf of Thailand, on the west coast in August and on the northeast coast in October and January; slight upwelling occurs all the year round at 12°N and 101°W. Off South Vietnam upwelling occurs during the summer monsoon between the central south Vietnamese coast at Nhatrang for some hundreds of miles up the coast (Wyrtki, 1961). Wyrtki also suggests that upwelling should be found in the Banda Seas, Flores Seas and in the east Arafura Sea, during the southeast monsoon.

Areas have been estimated for the Indonesian upwellings. Those off Java and northwest Australia are taken from the surface temperature distributions in Wyrtki (1964). Those in the Gulf of Thailand and off Vietnam are from the Naga expedition results (Wyrtki, 1961). Those in Flores, Banda and Arafura Seas are estimated from the sea area, in the absence of surface temperature observations showing upwelling, and are hence overestimated. Wyrtki bases his judgment on some sections, which have been used to make the estimate.

Minor upwellings

The Inter American Tropical Tuna Commission has studied a number of gulfs on the west coast of Central America in its search for live bait for tuna. Local upwelling has been found in the Gulf of Panama (Schaefer, Bishop and Howard (1958) and the Gulf of Venezuela (Redfield, 1955), in each case generated by offshore winds. Similarly Garner (1961) has described coastal upwellings off Cape Reinga and off the northeast coast of the South Island in New Zealand. Such areas will be found in other areas of the world when detailed study becomes possible.

7. CARBON PRODUCTION

There are many measures of primary production. Since the question of respiration in radiocarbon measurement was resolved by Steemann Nielsen and Hansen (1959) and the problem of calibration was dealt with by Steemann Nielsen (1964) and by Goldman (1968), most of the doubts raised about the method in the fifties have disappeared. Further, Koblents-Mishke (1965) has combined the surface observations (in $mgC/m^3/d$) with those at a number of depths in the photic layer ($mgC/m^2/d$); her regression has been used in this paper to convert surface observations in $mgC/m^3/d$ to $gC/m^2/d$. Given an adequate average estimate of $mgC/m^2/d$, the seasonal or annual production can be readily calculated.

The data used are those of Steemann Nielsen and Jensen (1957), from the Galathea Expedition in the Atlantic and Indian Oceans, Ryther et al., (1966) from the Anton Bruun to the Indian Ocean Expedition, and Kabanova (1964) from the Vityaz in the Indian Ocean. The summaries of the Pacific Ocean data of Koblents-Mishke (1965), Blackburn (1966) and Angot (1961) have been used extensively. Forsbergh and Joseph (1964), and Holmes, Schaefer and Shimada (1957) give observations made off Peru, northern Chile, in the Costa Rica Dome and in the equatorial region. Doty (quoted in Angot, 1961) has made many measurements in the Indonesian region, which (however) are higher than those of Steemann Nielsen and Jensen and Angot made in the same region, so his measurements have not been used.

Figure 15 gives Koblents-Mishke's figure of production in the Pacific as $mgC/m^2/d$. This figure shows the high latitude divergences, north and south, the Californian upwelling, the Peruvian upwelling and that off northern Chile. The extensive region of divergence in the eastern tropical Pacific extends into the zone of production along the equator. This is the region of divergence in the South

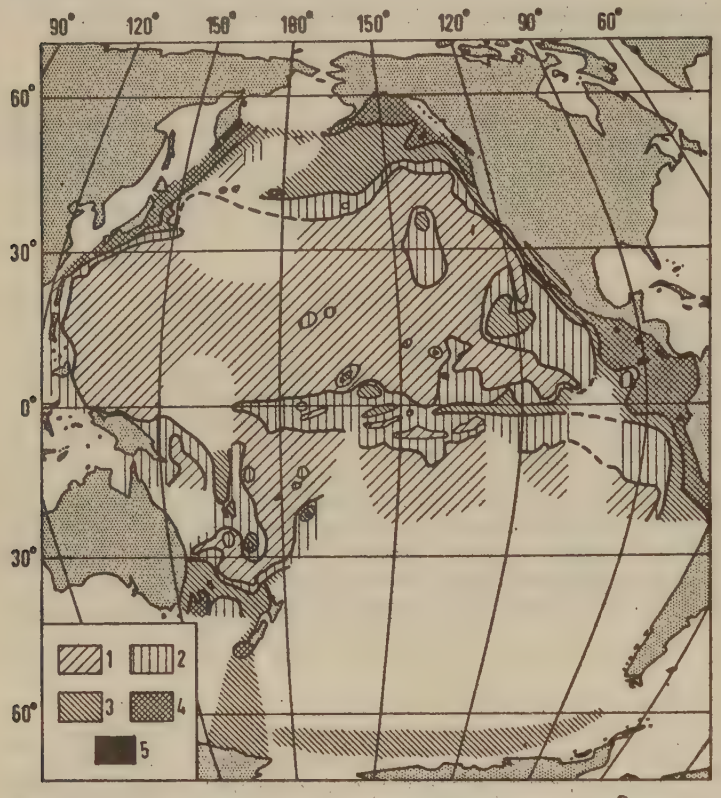

Figure 15. Distribution of production, in $mgC/m^2/d$, in the Pacific (Koblents-Mishke, 1965)

Equatorial Current, and east of 140°W, i.e. above the Cromwell Undercurrent. The productive areas near New Guinea and the Philippines are shown, as well as productive areas off Australia and New Zealand and off Japan.

In the Atlantic, there are some observations on the African coast, mainly from the Galathea Expedition. There are a few observations in the two southern areas of the Canary upwelling during November. In the Benguela Current there is adequate coverage in all four regions during the period December to January, sampling the main period of upwelling. In the Indian Ocean there are observations from Vityaz and the Anton Bruun covering the Somali Current, the southwest Arabia upwelling and the Madagascar wedge during the period of upwelling. They are supported by other observations summarized in Wooster, Schaefer and Robinson (1967). Off Orissa, there are only three observations from the Vityaz and off the Andaman coast there are only two, which are not enough to estimate a proper average. In the Indonesian area, including the South China Sea, there are observations taken on the Galathea Expedition and a number summarized by Angot (1961). The Japan Science Council, National Committee for IIOE (1966) has also summarized some observations off Java and northwest Australia. There are a few observations in each of the Flores, Banda and Arafura Seas. There are a number of observations off Vietnam and in the Gulf of Thailand.

In Table I the radiocarbon observations are classed and averaged by the upwelling areas. The observations by the areas and season set out in section 4 were expressed as a single average for the upwelling area. Treating the sampling as adequate in each region (which it is not, off Orissa or off the Andaman Islands), the area in km^2 is given with the duration of the season in days (from section 6); the production of carbon in each upwelling area is then given as tons $C.10^6/yr$. The figures have then been rounded off to the levels of 3, 5, 10, 20 and 50 tons $C.10^6/yr$.

Steemann Nielsen (1964) has found that the original method of standardization underestimated the true production by 45 per cent and his estimate has recently been confirmed by Goldman (1968). Nearly all the observations reported here contain the same error, based on a linear extrapolation of the self-absorption curve; it was not considered practicable to search for the few observations that might have been standardized with a different method. A general correction is therefore made in column E of Table I. The final result in each region is really an average figure of carbon production, raised by area and season. There are not enough observations to establish seasonal cycles in the upwelling areas.

From Table I it will be seen that the differences in $mgC/m^2/d$ are less than those in $tons.10^6/yr$. This is really only to be expected, because the differences are due to area and length of season. The Indian Ocean upwellings are less important than the four major upwellings because the season is limited to one monsoon – but the steady persistence of the monsoon winds makes the southwest Arabian area, at least, more important than, for example, the Californian area.

Confidence limits have not been calculated for each area, for two reasons: (1) there are not enough observations to establish seasonal trends which are important in some areas, (2) in some areas, e.g. the Canary Current, the Bay of Bengal and in some parts of the Indonesian area, observations are few. However, with the exception of those observations off Orissa and the Andaman coast, there are enough observations to establish fairly reliable means.

Although the 278 tons C.10^6/yr in the Benguela Current may not differ from the 155 tons C.10^6/yr in the Peru Current, the two quantities do differ from the 30 tons C.10^6/yr estimated for the California Current, and 35 tons C.10^6/yr off southwest Arabia. Column F in Table I gives rounded figures of 5, 10, 35, 75 tons C.10^6/yr (amongst others) which probably express real differences. So the Peru and Benguela Currents are the main upwelling areas (75.10^6t C/yr +), with California, southwest Arabia, Chile, New Guinea, Java and Vietnam as intermediate areas (ca30.10^6t C/yr), and the Somali Current, Costa Rica Dome, Madagascar Wedge, Orissa coast and the Indonesian areas as minor ones (5-10.10^6t C/yr).

8. THE PRODUCTION OF ZOOPLANKTON

Many hauls for zooplankton have been made in the Pacific and Indian Oceans. Those made in the Pacific are well summarized by Reid (1962b), and those in the eastern tropical Pacific by Blackburn (1967). The metre nets were hauled from about 200 m to the surface (ranging from 100 m to 300 m on some occasions) and the catches were expressed as ml/1000 m^3 displacement volume. Observations in the Peru Current were confirmed by the large quantities of information on Hensen net hauls from 50 m to the surface (Flores, 1967; Flores and Elias, 1967 and Guillen and Flores, 1967). The mesh size of the metre nets was usually about 0.25 to 0.31 mm and the net was hauled at about 1 m/sec. So a proportion of the zooplankton population escaped through the meshes and a further proportion evaded capture. Further, it is possible that the displacement volume included an unspecified volume of algae. There is no information about the mesh selection of these nets with respect to the composition of the displacement volume. It is hoped that the loss of zooplankton through the meshes is balanced by gain of algae by clogging. Loss by escape has not been measured, although shown for some larger animals (Fleminger and Clutter, 1965; McGowan and Fraundorf, 1966), so it is possible that euphausiids everywhere are improperly sampled. However, with the present state of zooplankton sampling, the nets used probably represent the best compromise for estimates of zooplankton displacement volume over extensive areas. To count the animals and estimate their volumes from an array of nets, each sampling a band of size properly, would take so much time that the results could not have been obtained as quickly for such extensive areas.

In the Indian Ocean, Wooster, Schaefer and Robinson (1967) gives samples from a 0.200 m water column from the Indian Ocean standard net, which is like that used in the Pacific, with a mesh size of 0.33 mm and a mouth opening of 1 m^2 (Currie, 1963). The Indian Ocean net was hauled off Somali and southwest Arabia in strong winds and so an average wire angle of 45° has been assumed (from my own observations on R.R.S. DISCOVERY). A similar net was used by Tranter (1962) off northwest Australia and off Java. The Russians working in the Indian Ocean have used a large Juday net (0.5 m^2, with a mesh of 0.26 mm) and they express their results as mg/1000 m^3 wet weight, essentially the same form of expression as used in the American and Australian work. Tranter (1963) has shown that the Juday net with a mesh of 0.26 mm catches more than the Indian Ocean net, with a mesh size of 0.33 mm but it is not stated whether the added living material was of nauplii or algae. Frontier (1963) has made some observations in the Guinea Current off Abidjan with a Hensen net (0.33 m^2; 0.41 mm mesh). There are unfortunately no observations of zooplankton made in the Canary Current or in the Benguela Current except those made on the Meteor Expedition. On that expedition numbers of "metazoa" were counted from 4 litres of water taken at the surface, at 50 m and 100 m (Hentschel, 1933). Kamshilov's (1951) formula converting length (0.6-1.0 mm) to weights for copepodites (0.6-1.0 mm) and nauplii (0.08-0.1 mm) has been used. This procedure gives results which are comparable with those from other upwelling areas. Therefore the Pacific and Indian Ocean nets appear to sample the zooplankton populations adequately, excluding larger forms like euphausiids which were not caught by Hentschel's waterbottles. However, the two methods are so profoundly different that they are separated all through the estimating procedures.

If possible the estimates of the stock of zooplankton as ml/1000 m^3 should be converted to measures of production. The first step is to determine the depth from which the nets were hauled, so that ml/1000 m^3 are converted to ml/m^2 in a specified layer; fortunately the authors quoted above give the depths of sampling in the upwelling areas specified. An upwelling area might be 800 km in length by 200 km in width, with a current moving towards the equator at 20 km/d (Wooster and Reid, 1963). So there is an input of zooplankton from the poleward end and it is generated from the coast by upwelling. Very roughly it takes one zooplankton generation for water and zooplankton to be drifted across the length of an upwelling area. The survival of animals across the upwelling area depends on the algal production. So we may consider the generation of zooplankton to be autonomous within the upwelling area. The production of zooplankton is given by the average standing crop as ml/m^2, multiplied by the number of generations during the upwelling season.

Marshall and Orr (1955) give the duration of copepodite stages as a proportion of the duration of copepodite stage I. McLaren (1965) gives the duration of some copepodite stages at different temperatures, so a relation between stage duration and temperature was constructed. On the basis of data given by Marshall and Orr (1955) on maturation and hatching, the duration of a full generation could be worked out at different temperatures. They do not differ much from the estimates of Heinrich (1961). The estimated generation time has been arbitrarily lengthened by one third, to take account of the intermittent character of upwelling, due to variation in the wind stress (California, Department of Fish and Game, 1953). The zooplankton distributions off California (Thrailkill, 1956, 1957, 1959, 1961, 1963) reflect to some extent the transient structures of an upwelling region, possibly because the animals are vulnerable to food lack in the periods between upwellings. The same procedure should really be applied to the algae, but a short half of a week or so only reduced the rate of increase of algal production, whereas a week's halt in upwelling may cause the failure of a local brood of nauplii, and when upwelling returns it would take half a generation for a new brood to get underway. The estimate of one third of the generation time was taken from the seasonal picture of intermittent upwellings off Southern California (California, Department of Fish and Game, 1953).

It is possible that the intermittent halts in the upwelling process actually sustain greater levels of production. The rate of increase of algal production is reduced and the zooplankton production is perhaps destroyed. Where the upwelling is resumed, the algae continue to produce, but the grazing restraint is no longer there. So a new outburst is possible until the zooplankton has been regenerated. The available data in different areas are not good enough to support or deny this speculation.

In Table I, where the data are presented in detail, column L gives the generation time with one third added. In all the upwellings examined, temperature observations at the surface are available from the sources given in section 6. b. Only in a few cases can the observations be averaged adequately through a season, but they are well enough established to estimate generation time. Columns N_1 and N_2 give the total secondary production as tons $C.10^6$/yr, with the lengthened generation time (N_1) and with an uncorrected generation time (N_2), so the quantity in column N_2 is one quarter greater than that in N_1. The quantity ml/m^2 (or g/m^2, wet weight) is converted to ^{2}carbon by the factor 1/17.85 (Cushing, 1958). This figure, raised to the area of the upwelling area (as defined above) and raised by the number of generations (as defined above), gives the quantity produced, in tons C/yr.

The secondary production in tons $C.10^6$/yr is given in Table I. Although there is a large quantity of information on secondary production in the California Current, observations in other upwelling areas are sufficient only to establish an average, but not a seasonal trend, as for the radiocarbon measurements. The most important upwelling areas in terms of secondary production are those in the Peru Current and the Benguela Current, where production is of the order of $3\text{–}5.10^6$ tons C/yr (using column N_1). The production in other upwelling areas for which there is enough information is around $1\text{–}2.10^6$ tons C/yr. There is not enough information to draw any conclusion for the Canary Current in secondary production and that for the Guinea Current is based on very few observations. For many areas for which radiocarbon observations are available, there are not adequate observations in zooplankton. However, the southwest Arabian upwelling, the Domes off Costa Rica and Java and the Indonesian area appear to be areas of medium zooplankton production. So far as it goes this arrangement of high production in the Peru and Benguela Currents and medium production in other areas does correspond to the order given for the radiocarbon measurements.

Summarizing, the estimates of secondary production are based on the use of one standard net, or its analogues. In fact a number of different designs have been used (see Reid's table 2) but the differences are not great enough to generate differences in quantities caught. Indeed the very meticulous methods used by Hentschel on the Meteor Expedition tend to confirm the results from the CALCOFI/POFI/IIOE nets. Perhaps the assumptions that the loss of nauplii is balanced by gain of algae, and that the proportions escaping are small, are roughly justified.

9. TROPHIC LEVEL EFFICIENCY AND THE THIRD TROPHIC LEVEL

The results in Table I can be used to make an estimate of the efficiency of transfer from one trophic level to another. The primary production is expressed in tons $C.10^6$/yr produced and so is the secondary production. The efficiency of energy transfer is given by the ratio of secondary production to primary production and the percentages are given in columns O_1 and O_2; in column O_1 the trophic level efficiency with a "lengthened" generation time of secondary production is given, and in column O_2 that with an uncorrected generation time is shown. The estimates in column O_2 are higher than those in column O_1. They range from 1.44 per cent to 23.67 per cent (or 1.92 per cent to 31.51 per cent), and the average is 9.75 per cent (O_1) and 13.09 per cent (O_2). There is no evidence of a trend with temperature or with latitude. It should be pointed out that the higher value of trophic level efficiency is derived in the simpler way by merely taking the number of generations and not the lengthened generations. The efficiency (13.09 per cent) is a little higher than the 10 per cent usually accepted. The method with the lengthened generation time yields an efficiency of 9.8 per cent. The efficiencies of conversion in the Pacific upwelling areas, excluding the eastern tropical sector, New Guinea and the Marquesas areas, are higher (13.89 per cent and 18.53 per cent) than in other areas. Because of the fair uniformity of method over extensive areas, it is possible that the Pacific estimates are the best ones. Hence a figure of more than 15 per cent in the upwelling areas is a distinct possibility.

The production at the third trophic level may be estimated by taking 1 per cent of the primary production or 10 per cent of the secondary production by both of the estimates used. The estimates are given in Table I. Where possible an average has been taken of 1 per cent of primary production and 10 per cent of the secondary production, with the two methods used. This average has been expressed as tons $C.10^4$/yr and as tons wet weight/yr. The two estimates proceed from independent estimates of primary and secondary production respectively, but both make an assumption of 10 per cent efficiency between secondary and tertiary production. They are not therefore entirely independent, but the degree of correlation between them suggests that the basic methods are sufficient for our present purposes. The weights from the Marquesas divergence and the eastern tropical Pacific are excluded from the sum because the oceanic production cycle has a third trophic level composed of very small fish, for example, the myctophids of the Deep Scattering Layer. It is assumed that these fish should not be exploited at present because they are widely dispersed and costly to catch. The sum of third level production available in coastal upwellings (as opposed to equatorial upwellings) is about 125–150 M tons wet weight per year. If the true transfer coefficient of energy is higher, for example, 15 per cent, the the available production in the third trophic level should be increased to 190–300 M tons wet weight/yr.

The question which now arises is how much of the third trophic level is composed of fish. In temperate waters the competitors with fish at the third trophic level are carnivorous copepods, arrow worms, jellyfish, ctenophores, squids and other pelagic molluscs. So the weight of secondary production in Table I includes part of the third trophic level as invertebrates. Very little is known of the abundance of squids and since they are in economic and fishery terms comparable with fish they will be treated as fish. To account for part of the invertebrate third trophic level, 9 per cent of the secondary production is taken, and the tertiary production would then amount to about 120 M tons or ca 210 M tons at a 15 per cent conversion rate. All estimates given here are averaged across the upwelling area and through the whole season.

If the tertiary production is largely composed of fish and squid, then the annual production is the annual increment to populations in recruitment and in growth. It is assumed that the maximum biomass of a fish stock is reached during adult life, because from one generation to the next the weight of gonads in the stock must increase by three or six times to create the filial stock. Fish in sub-tropical areas do not appear to live very long. Peruvian anchoveta live for 2 to 3 years and Californian and South African sardines live for 3 to 6 years (Davies 1958, Marr 1960). Hake, which feed on euphausiids, may live somewhat longer. A rough effective life span in the fishery of about three years would be reasonable. Hence the stocks available in the upwelling areas might range from 340 M tons upwards and the yield, to all consumers of the tertiary production, of which man can probably take no more than half, equivalent to one year's recruitment, ranges from 113 M tons upward.

This result is above most present prognostications for world fisheries, save that of Chapman (1967). It includes all fish in the pelagic zones, – sardines, anchovies, scads, hakes and part of the tuna-like fishes. Although the proportions are known off California, the same proportions may not apply elsewhere. — For example, in the Peru Current, egg samples taken throughout the year show that the anchoveta out-numbers all other species at all seasons by a factor of ten. In some distributions, the eggs of other species are excluded in space by those of the anchoveta. Off California, the eggs of sardine and anchovy at the coast and jack mackerel and hake are distributed in succeeding bands offshore, hake and

anchovy abundant and sardine less so (Ahlstrom, 1966; Alverson, 1967, California, Department of Fish and Game, 1956). The two best known areas, Peru and California, are so profoundly different that no generalization can be made about the division of the annual third level of production into groups of fish.

Most production of harvestable animals in the upwelling areas is tertiary, but that in the divergences of the equatorial region is in the fourth level, the larger tuna-like fishes feeding on a level of small fish and macrozooplankton. In the eastern tropical Pacific and in the Marquesas divergence the production at the fourth level, may be estimated as 95 and 30 tons $C.10^4/yr$, or 1.6 and 0.5 tons wet weight/yr.

The tuna stocks are oceanic and the larvae are distributed all over the ocean. Hence the stocks need not depend upon the divergences of the coastal upwellings or the equatorial system to sustain themselves and it would be difficult to disentangle the contribution from the upwelling areas. However, the low oceanic catches of tuna are explained. A very rough estimate of the total production of tuna-like fishes in the world ocean would not be greater than perhaps 3-5 M tons in the equatorial region.

Columns S_1 and S_2 of Table I give the wet weights of tertiary stocks in M tons/year. It will be seen that the major areas are those in the Peru and Benguela Currents (about 20-30 M tons). The medium areas are California, Chile and southwest Arabia (5-10 M tons). The rest are small ones (1-5 M tons). Gulland (1968) has suggested that the total annual deaths (equal to total annual production) of the anchoveta stock off Peru is 18-20 M tons. As there is now only one year-class in the stock (and most of our carbon and zooplankton observations were taken during the period of exploitation), the correspondence between Gulland's estimate and this one is quite good.

Taking all upwelling areas, the production of fish and squid may be as much as 120-130 M tons. If we suppose that one third to one half can be taken by fishing, then a potential catch of 40-60 M tons is available. As some of this catch (ca 15 M tons) is already being taken, perhaps we may guess that a further 25-50 M tons of fish and squid can be taken from the upwelling areas.

10. THE BIOLOGY OF AN UPWELLING AREA

Fishes characteristic of an upwelling area are not caught outside it. As the stocks are maintained within it from year to year, it is reasonable to suppose that an upwelling area is a biological unit. The fact that the water necessarily drifts through the area does not mean that the biological structure is a temporary one, but that the fish stocks do maintain their position in it from year to year. Off California, hake spawn in the early spring off the southern area of upwelling (Ahlstrom 1966). The older fish appear off the coasts of Oregon and Washington in June (Alverson, 1967). As they live mainly in deep water (i.e. 200 m) , they may migrate north in the countercurrent. To spawn off Baja California, the hake may return south in winter in the surface drift, perhaps at night when the hake are known to migrate towards the surface. Presumably the eggs and larvae drift south from Baja California and metamorphose fairly quickly to sink into the countercurrent, which persists until the summer. Then the nursery area may lie at a middle depth off Central California. So the fish might live in the upwelling areaall through their lives. Although this argument is in detail speculative, the main points emerge from a figure in Alverson (1967).

The Californian sardine spawns right in the coastal upwelling zones, as physically defined, off Punta S. Eugenio and between Point Conception and San Diego. The anchoveta in Peru spawns between Punta Aguja and San Juan in late winter to early summer, when the Ekman transport is most intense (Wooster and Reid, 1963). The greatest densities of eggs are found within 100 km of the coast where the radiocarbon values are highest (Forsbergh and Joseph, 1964). So the Californian sardine and Peruvian anchoveta spawn near the line of upwelling. They live in or near the thermocline and so cannot make use of the Countercurrent in their migration. However, there is sometimes a very narrow coastal Countercurrent during the season of upwelling (Reid, Roden and Wyllie, 1958; Wyrtki, 1963). The fish spawn in late spring and early summer. Hence one might expect them to drift away from the spawning ground close to the coast in the coastal Countercurrent. Then the fish can return to the spawning ground in the surface drift of the California Current. There were three groups of sardine off California, perhaps one in each upwelling section (Clark and Marr, 1955).

There is a remarkable phenomenon in the Peru Current upwelling. It is that the spawning anchoveta (as shown in the egg distributions) appear to exclude the zooplankton, Figure 16. The inverse correlation is not exact, which may suggest that there is a time lag in its generation.

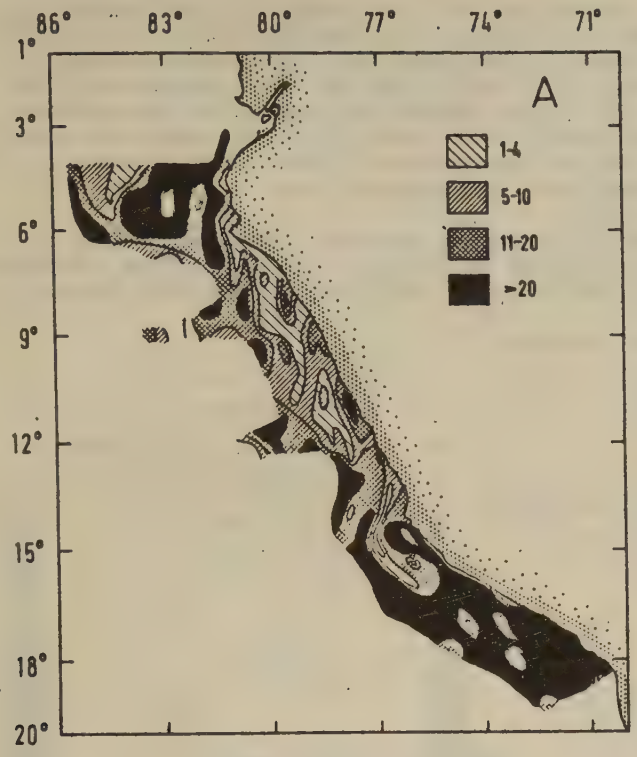

Figure 16(a)

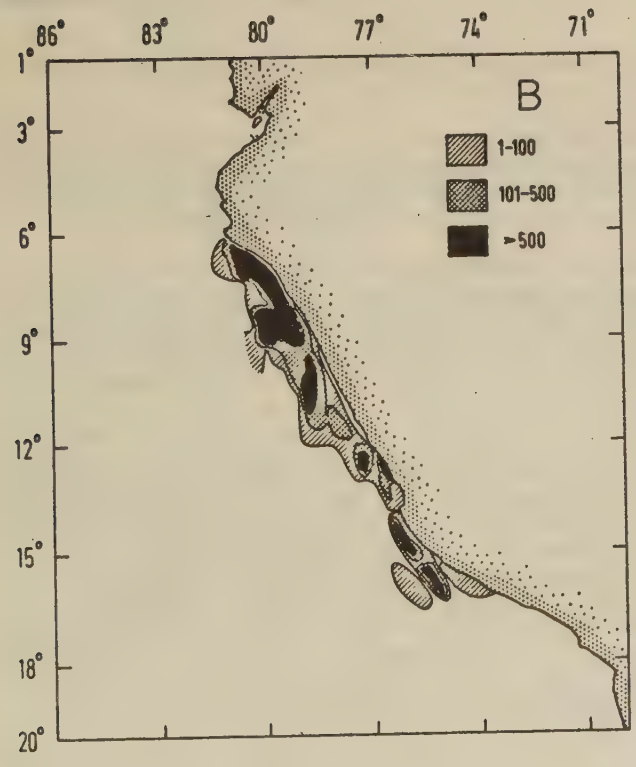

Figure 16(b)

Figure 16. The distribution of anchoveta eggs and of zooplankton off Peru.

(a) Distribution of zooplankton in ml/haul, displacement volume;
(b) Distribution of anchoveta eggs in numbers/haul with a Hensen net (Flores, 1967; Guillen and Flores, 1967)

There are alternative explanations: (a) that the spawning anchoveta eat algae (as its relative, Centengraulis mysticetus does in the Gulf of Panama, Bayliff, 1963) and that the anchoveta aggregate on the algae, competing with the zooplankton; (b) that the anchoveta, like the European anchovy, selects small copepods, but traps algae on its narrow gill rakers; then the spawning anchoveta has eaten the zooplankton animals before they spawn. The latter explanation implies that the anchoveta is at the third trophic level. The stripping of zooplankton from the water by the anchoveta may allow a new production cycle to start after the fish disperse from the spawning ground. This process resembles that postulated in an intermittent upwelling area, as suggested above.

The vertical distribution of animals in an upwelling area has a special interest. Figure 17 shows the distribution of echo traces off Peru, presumably of anchoveta, in the thermocline (Flores and Elias, 1967). The thermocline is rather weakly defined, but the fish remain in the upper part of it.

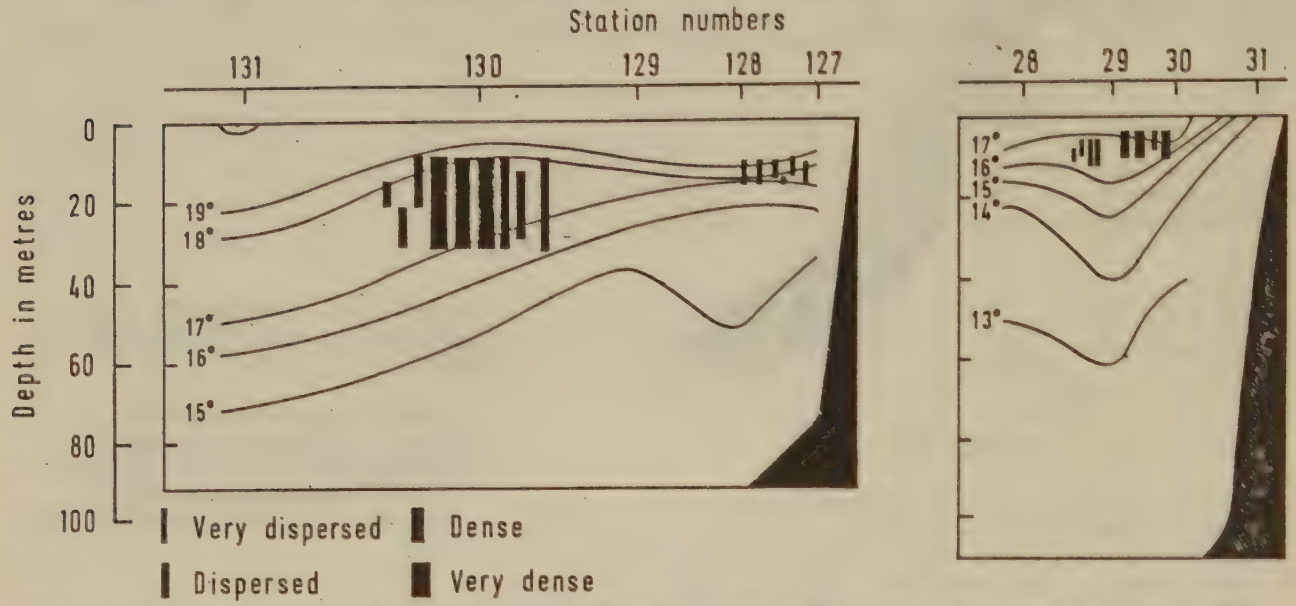

Figure 17. The distribution of echo traces in the thermocline off Peru (Flores and Elias, 1967).

Sardines, sardinellas and anchovies live at or just above the depth of the thermocline. Below the thermocline live horse mackerel, probably in extensive and rather dispersed shoals. On the bottom at any depth of water from 50 fathoms outward hake live close to the bottom, perhaps depending to some extent upon euphausiids, the biology of which has been little studied in an upwelling area.

In this section, some of the biological problems in an upwelling area have been posed in a speculative manner. They have been grouped together because it is thought that any upwelling area is a biological unit, worthy of investigation in itself. Because the fisheries in the upwelling areas are large and important, the methods of fisheries biology applies to upwelling areas should yield results of wider import.

Discussion

The methods used in this paper depend primarily upon the physical description of upwelling area and season. It was assumed that the biological zone of production was two and a half times wider than the apparent physical one. This ratio may differ in areas other than that off California; indeed that of Peru may be much wider. The radiocarbon estimates are probably good when sufficient are available. The zooplankton observations are vulnerable to excape, loss through the meshes and the irrelevant capture of algae. But the correspondence of other observations seem to justify the assumptions. The most important check is that 1 per cent of the primary production corresponds with 10 per cent of the secondary production - estimates which are independent. Lastly the estimates of third level stock off Peru are not very different from that made by Gulland (1968) for the anchoveta stock there. Despite the roughness of the methods used there appears to be a consistency in the results.

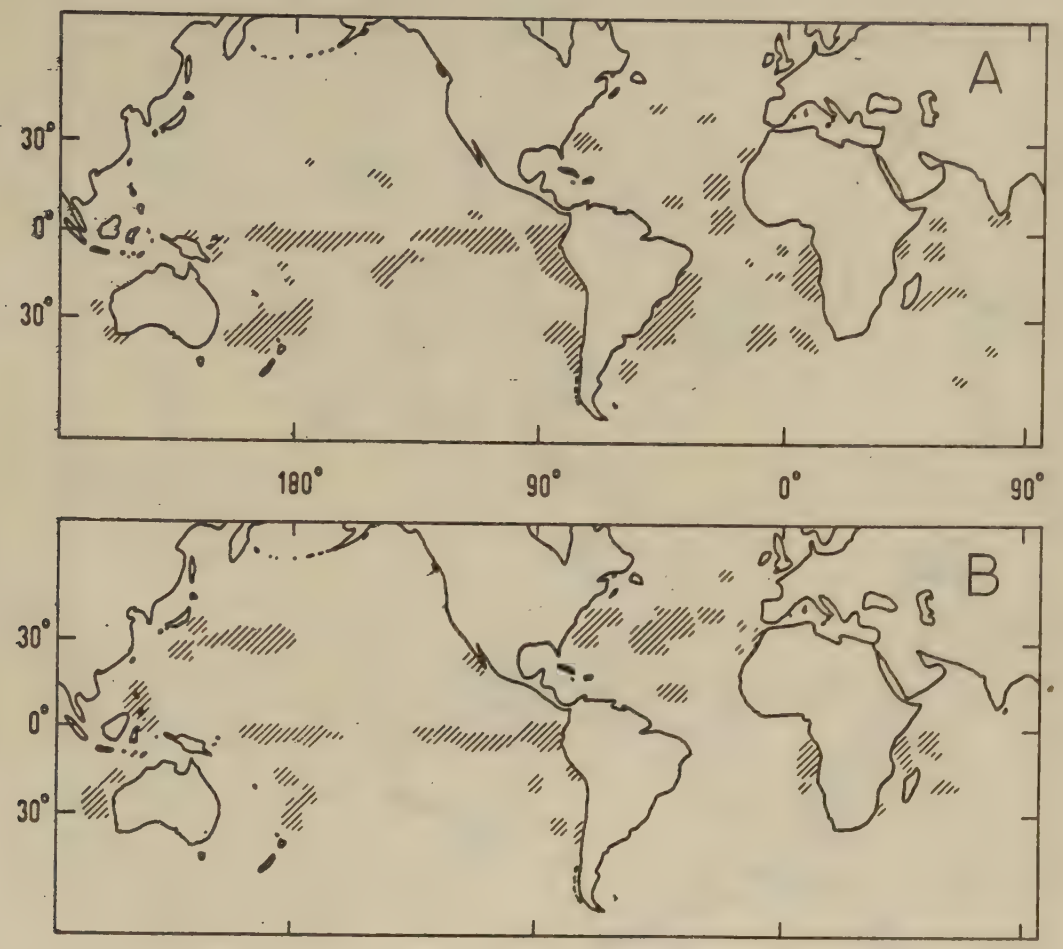

Figure 18. Distribution of sperm whale catches from Nantucket 1726–1919, (Townsend, 1935);
(a) northern summer
(b) northern winter

The areas of upwelling in the broad sense can be charted, but they can also be indicated indirectly. Figure 18 shows the positions of capture of sperm whales by Nantucket whalers from 1726 to 1919 (Townsend, 1935). It will be seen that the main upwelling areas, California, Peru, Benguela and Canary are indicated. That off northwest Australia is more noticeable than would be expected from other physical and biological evidence. The most striking area of capture is that along the Line in the Pacific in the South Equatorial Current. In the southern winter these areas remain as the Peru Oceanic Current divergence and that in the western ocean. The Madagascar Wedge appears on the chart (in the northern summer) and so does the divergence southeast of Ceylon. The New Guinea divergence can be seen as well as an indeterminate area between the Philippines, Borneo and the Celebes. The Canary Current extension in winter is noticeable and so are the northern divergences, particularly those in the Kuroshio extension in winter. The only anomaly on the chart is really the area in the Gulf Stream and central North Atlantic in summer; perhaps in the two areas there was a concentration of vessels coming from easterly or westerly into Nantucket. Absent are the Somali, South Arabia, Orissa and Vietnam upwellings.

Another way of showing the world upwelling areas is in a chart Figure 19 of the phosphatic deposits (Tooms, 1967). All the main upwellings are shown even small ones like those off the Malabar coast and off the southern coast of Ceylon. The Guinea upwelling is shown and so is that off northwest Australia. The deposits off South Africa extend round the Cape of Good Hope to Cape Agulhas and beyond. It is known that upwelling can continue offshore round the Cape but it would be surprising to put it at the same level as that off the western coast of South Africa. The deposit off California suggests that the centre of upwellings is really between Cape Mendocino and Point Conception and that the present shift southward to Baja California is perhaps a climatic deviation (California, Department of Fish and Game,

Figure 19. Distribution of phosphatic deposits (Tooms, 1967)

Figure 20. Distribution of guano islands (Hutchinson, 1950)

1953). The equatorial system is not shown at all by this method, but the form of production cycle there has not the disbalanced nature needed to spill phosphorus on the seabed. Nothing is shown for the Indonesian area or the Caribbean, perhaps because the upwelling is less intense or nearer the steady state of the tropical ocean.

A third method of showing the upwelling areas is by charting the Guano Islands (Figure 20, adapted from Hutchinson, 1950). Islands are needed, but in Peru capes and points are used by the birds. The more important upwelling regions, Peru and Benguela, are clearly shown. The Somali and Southern Arabian ones are indicated and so are the Indonesian ones, particularly the Banda Sea, the New Guinea divergence, northwest Australia and the areas off Vietnam and Borneo. The Californian area is shown only off Baja California and in the Gulf of California although there are many islands to the north, particularly just south of Point Conception. There is no sign of guano islands in the Canary Current although islands are available. Perhaps, over a long period, the California and Canary Currents are not intense enough or are too variable to support the population of birds. A surprising point is the indication of upwelling in the Madagascar Wedge and off Venezuela. There are few guano islands in the Indian Ocean, but there are some on the south coast of Australia.

The nature of the upwelling process has been described physically, but not biologically. The vertical velocity has been estimated by a number of authors, but it has not been measured nor has it been related to biological production, save in one instance. In the Costa Rica ome, Wyrtki (1964) has estimated the vertical velocity from a heat budget. The difference between the surface concentration of phosphate phosphorus and that below is raised by the upwelling velocity to give the daily use of phosphate. It is rather close to the daily carbon production as measured by the radiocarbon method. The surface value of phosphate is unbalanced in this sense, i.e. a greater proportion has been absorbed than regenerated and this proportion changes with distance from the line of upwelling and so phosphorus concentration declines offshore. But just as the temperate production cycle can be analyzed in its unbalanced state, so can that in an upwelling area. But the relationships between upwelling velocity, nutrient consumption, grazing and production need disentangling.

Apart from the theoretical work of Hidaka and Yoshida the study of upwelling has been in the first stage of exploration and description. There is a second stage in oceanographic research where a survey should be mounted in sufficient detail to allow a more analytical approach to be sustained. For such a survey an area can be defined by the zone of biological production in width and its homogeneous seasonal production in length (for example, one of the three areas off Western North America such as that from Point Conception to Baja Californai). Physical measurements can be taken by continuous recording, for example, of temperature, salinity and oxygen. Measurements of phosphate, nitrate, silicate, nitrite, chlorophyll and turbidity can be made continuously with Autotechnicon methods (Armstrong, Stearns and Strickland, 1967). Radiocarbon measurements are needed, together with zooplankton hauls above 200 m and below 200 m, with high speed tow nets (Beverton and Tungate, 1967). The same gear can be used for fish eggs and larvae. High resolution acoustic gear can be used for all depth strata, together with means of catching at any depth for identification.

Observations such as these could be made on a routine survey basis in a unit upwelling area as defined above. The observations must be made frequently enough in time to follow the dynamic changes, regularly perhaps two to three cruises a month. The types of ship employed should include a stern trawler equipped for research purposes, because of the need to catch fish adequately at all depths.

At the same time particular problems should be studied from other research vessels, for example, the detailed processes of the upwelling system, production and rate of upwelling, vertical migration of fish with respect to the thermocline, the dependence of fish stocks on available food, etc. It goes without saying that the fisheries in the upwelling areas must be examined fully during the period of survey. Catch and effort statistics must be adequate, fecundity estimates made and the fishing mortality estimated.

This is not a plan of campaign, but a sketch to show what is needed. A stern trawler with research facilities could cover such an area about twice a month on a coarse scale and once a month in greater detail. Such a ship is needed for its catching capacity for fish. A smaller ship could be employed at the same time on the special problems. Much of this sort of work has been done off California or off Peru already but it has not had the sustained quality that is needed. Nor has the combination of survey vessel and specail problem vessel been exploited to the degree that the importance of the problem warrants.

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TABLE I. Annual primary, secondary and

	PRIMARY PRODUCTION						SECONDARY					
	A	B	C	D	E	F	G	H	J	K	L	M
	mgC/m²/d (a)	gC/m²/d	Area ($km^2 . 10^3$)	Season (days)	Carbon tons/yr (a) 10^6	Carbon tons/yr 10^6 (rounded)	ml/1000³ displacement volume	Depth sampled (m)	ml/m²	gC/m²	Generation time (days)	Number of generations
Pacific												
California 1	250	0.250	169	180	11.03	10	200	140	28	1.57	52	3.46
2	161	0.161	106	180	4.45	5	300	140	42	2.35	61	2.95
3	250	0.250	230	180	15.01	15	500	140	70	3.94	68	2.65
Costa Rica Dome	260	0.260	148	300	16.73	15	300	300	90	3.36	31	9.67
E. Tropical	175	0.175			1245.55			300			31	
Peru 1	325	0.325	288	270	36.64	35	225*	300	68	3.78	52	5.18
2	1020	1.020	191	270	76.27	75	200	300	60	3.36	52	5.18
Chile 1	242	0.242	375	270	35.53	35	150	300	45	2.52	52	5.18
2	205	0.205	150	180	8.03	10	500	300	150	8.44	68	2.65
Marquesas	135	0.135	8760	300	514.46		75	200	25	1.41		
N. Guinea	205	0.205	460	300	41.04	40	150	200	30	1.68		
Atlantic												
Canary 1	400	0.400	40	150	3.48	3	375	200	75	4.20	52	2.89
2	390	0.390	105	205	12.19	10	375	200	75	4.20	52	3.94
3	(400)		306	180								
4	(400)		150	180								
5	(400)		90	150								
Guinea			100	120			315	200	63	3.55	31	3.87
Benguela 1	280	0.280	35	90	3.46	3						
2	1130	1.130	240	240	94.38	100	750	200	150	8.40	52	4.62
3	530	0.530	210	360	98.60	100	375	200	75	4.20	52	6.93
4	1560	1.560	144	240	78.15	75	320	200	64	3.58	61	3.94
Indian												
Somali	690	0.690	95	180	17.10	15	250	200	50	2.81	48	3.75
S.W. Arabia	1000	1.000	131	180	34.19	35	250	200	50	2.81	31	5.80
Madag. wedge	750	0.750	1014	180	8.66	10	530	200	106	5.97		
Orissa	415	0.415	96	150	8.67	10	213	200	43	2.42	28	5.36
Andaman	225	0.225					50	200	10	0.56		
W. Ceylon	410	0.410										
Indonesia												
Java	415	0.415	300	150	27.09	30	140	200	28	1.34	31	4.84
N.W. Australia	284	0.284	300	150	18.53	20	117	200	23	1.29	31	4.84
E. Arafura	390	0.390	250	120	16.97	15						
Flores	505	0.505	100	120	8.79	10						
Banda	650	0.650	100	120	11.31	10						
Gulf Thailand	1098	1.098	75	150	20.75	20						
Vietnam	1270	1.270	200	120	44.20	40						

* Holmes, Schaefer and Shimada (1957) quote 600 ml/1000 m³ Note (a) Carbon production in column A as published.

tertiary production in the upwelling areas

PRODUCTION				TERTIARY PRODUCTION						
N_1	N_2	O_1	O_2	P	Q_1	Q_2	R_1 $(P+Q_{1/2})$	R_2 $(P+Q_{2/2})$	S_1 R x 17.85	S_2 R x 17.85
Carbon tons/yr 10^6	Carbon tons/yr 10^6	Trophic effic.(%) N_1/F	Trophic effic.(%) N_2/F	Tons C. 10^4 $1/E$	Tons C. 10^4/yr $10^4/N_1$	Tons C. 10^4/yr $10^4/N_2$	Tons C. 10^4	Tons C. 10^4	Tons wet weight 10^6	Tons wet weight 10^6
0.90	1.20	8.16	10.88	11.03	9.0	12.0	10.00	11.51	1.79	2.05
0.74	0.98	16.63	22.02	4.45	7.4	9.8	5.92	7.12	1.06	1.22
2.40	3.19	16.00	21.25	15.01	24.0	31.9	19.50	23.45	3.48	4.00
2.26	3.01	13.51	18.00	16.73	22.6	30.1	19.66	23.41	3.52	4.05
69.18	92.01	5.54	7.39	1245.55	691.8	920.1				
5.64	7.50	15.39	20.47	36.64	56.4	75.0	46.52	55.82	8.30	9.55
3.33	4.43	4.33	5.81	76.27	33.3	44.3	54.78	60.28	9.78	11.25
4.89	6.50	13.76	18.30	35.53	48.9	65.0	42.21	50.26	7.53	8.66
1.90	2.53	23.67	31.51	8.03	19.0	25.3	13.51	16.66	2.41	2.77
18.40	24.47	3.58	4.76	514.46	180.4	244.7				
1.16	1.54	2.83	3.77	41.04	11.6	15.4	26.32	28.22	4.69	5.39
						Total Pacific (excl.E.Tropical & Marquesas)			42.56	48.94
0.49	0.65	14.08	18.68	3.48	4.9	6.5	4.19	4.99	0.75	0.86
1.74	2.31	14.27	18.87	12.19	17.4	23.1	14.79	17.64	2.64	3.04
									(5.7)	(5.7)
									(2.8)	(2.8)
									(1.4)	(1.4)
1.37	1.82				13.7	18.2	16.00	16.00	2.86	3.29
				3.46			3.46	3.46	0.62	0.71
1.36	1.81	1.44	1.92	94.38	13.6	18.1	53.99	56.24	9.66	11.11
6.99	9.30	7.09	9.43	98.60	69.9	93.0	84.25	95.80	15.04	17.30
2.03	2.70	2.59	3.46	78.15	20.3	27.0	49.22	52.57	8.79	10.11
						Total Atlantic			50.26	56.32
1.00	1.33	5.85	7.78	17.10	10.0	13.3	13.55	15.20	2.42	2.78
2.14	2.85	6.26	8.34	34.19	21.4	28.5	27.79	31.34	4.96	5.70
				8.66			8.66	8.66	1.55	1.78
1.25	1.66	14.41	19.15	8.67	12.5	16.6	10.58	12.63	1.89	2.17
									?	?
									?	?
1.95	2.59	7.19	9.56	27.09	19.5	25.9	23.30	26.50	4.16	4.78
1.87	2.49	10.09	13.43	18.53	18.7	24.9	18.61	22.71	3.32	3.82
				16.97			16.97	16.97	3.03	3.48
		9.79	13.09	8.79			8.79	8.79	1.60	1.84
				11.31			11.31	11.31	2.02	2.32
				20.75			20.75	20.75	3.70	4.26
				44.20			44.20	44.20	7.89	9.07
						Total Indian Ocean, etc.			36.54+	42.00+
							668.90	742.50	129.36	147.26

Recent studies (Steemann Nielsen, 1964) show these should be increased by a factor of 1.45.
The values in column E and later are based on corrected values.

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